Brewer's Sparrow (*Spizella breweri*): A Technical Conservation Assessment

Photo by Greg Lasley

**Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project**

January 13, 2005

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Holmes, J.A. and M.J. Johnson (2005, January 13). Brewer's Sparrow (*Spizella breweri*): a technical conservation assessment. [Online]. USDA Forest Service, Rocky Mountain Region. Available: http://www.fs.fed.us/r2/projects/scp/assessments/brewerssparrow.pdf [date of access].

ACKNOWLEDGEMENTS

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COVER PHOTO CREDIT

Brewer's Sparrow (*Spizella breweri*). Photograph by Greg Lasley. Used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF BREWER'S SPARROW

The Brewer's sparrow (*Spizella breweri*) is a sagebrush obligate that is often the most abundant songbird in sagebrush shrubsteppe habitats. This assessment focuses on the *S. b. breweri* subspecies, which is found in USDA Forest Service (USFS) Region 2. Brewer's sparrow is considered globally "secure" by the Natural Heritage Program because of its wide distribution across North America. However, according to the Breeding Bird Survey, Brewer's sparrow populations have declined by over 50 percent during the past 25 years. Brewer's sparrow populations within the states of USFS Region 2 have exhibited similar long-term declines; in fact, declines in Colorado and Nebraska have outpaced national trends. In South Dakota and Kansas, the species is considered "imperiled" by the states' natural heritage programs. The Brewer's sparrow is listed as a priority bird species in the Colorado and Wyoming Partners in Flight bird conservation plans and as a species of special concern by the U.S. Fish and Wildlife Service. As a result of these regional declines and the species' vulnerability to habitat loss, USFS Region 2 lists the Brewer's sparrow as a regional sensitive species.

Reported Brewer's sparrow population declines on the breeding areas are likely linked to extensive alteration of sagebrush (*Artemisia* spp.) shrubsteppe habitat. Though widespread, this habitat constitutes one of the most endangered ecosystems in North America due to extensive, ecologically transformative influences of livestock grazing, followed by alteration of natural fire regimes and invasion by exotic plant species, especially cheatgrass (*Bromus tectorum*). Loss and fragmentation of habitat due to agricultural, urban, suburban, energy, and road development also threaten the species.

Conservation and management of Brewer's sparrows in Region 2 should focus on creating and maintaining a sagebrush landscape that replicates conditions historically created by climate and natural processes, including fire frequencies. Because sagebrush habitats and their dominant disturbance processes likely vary across Region 2, a simple set of strategic guidelines for Brewer's sparrow management and conservation will not work. The Brewer's sparrow belongs to a group of species that appear to be especially sensitive to the effects of habitat fragmentation. They are most abundant in areas where shrubs occur in tall, clumped, and healthy stands. Creation and maintenance of these conditions will require managing at large spatial and temporal scales, and assessing at these larger scales, the cumulative impact of activities that fragment habitat.

Successful conservation efforts for Brewer's sparrows and sagebrush shrubsteppe communities will require new and innovative strategies. Region 2 sagebrush habitats represent a relatively small fraction of the Brewer's sparrow's sagebrush habitat, and management of these lands alone is unlikely to ensure the long-term population viability of the species. Therefore, it will be necessary to develop partnerships among other federal and state agencies, private landowners, and conservation organizations to ensure the long-term conservation of complex, biologically rich sagebrush ecosystems.

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INTRODUCTION

This species conservation assessment is one of many being produced to support the Species Conservation Project for the Rocky Mountain Region (Region 2), USDA Forest Service (USFS). The Brewer's sparrow is the focus of an assessment because it is listed as a sensitive species in Region 2, and information regarding the conservation of sensitive species is to be integrated into USFS planning and implementation. This species also serves as a management indicator species (MIS) on the Bighorn, Shoshone, and White River national forests in Region 2 (**Figure 1**). As barometers for species viability at the forest level, MIS serve two functions: 1) to estimate the effects of planning alternatives on fish and wildlife populations (36 CFR 219.19 (a)(1)); and 2) to monitor the effects of management activities on species via changes in population trends (36 CFR 219.19 (a)(6)).

This assessment addresses the biology of the Brewer's sparrow throughout its range, focusing on Region 2. The broad nature of the assessment leads to some constraints on the specificity of information for particular locales. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.
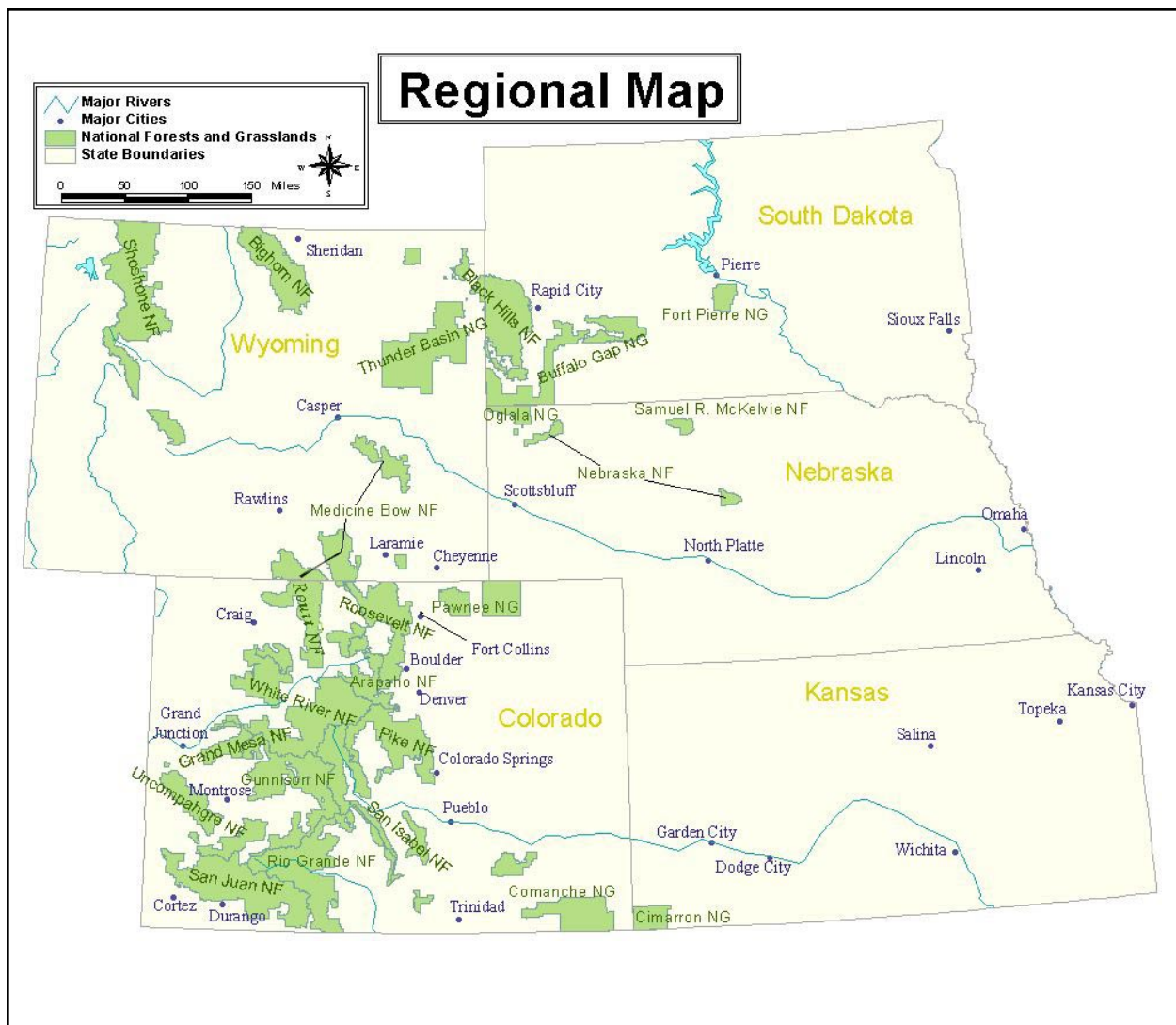
Figure 1. Regional map of USDA Forest Service Region 2. National grasslands and forests are shaded in green.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide managers, biologists, other agencies and organizations, and the public with a thorough discussion of the biology, ecology, conservation, and management of certain species based on current scientific knowledge. These assessments do not seek to develop prescriptive management recommendations. Rather, they provide the ecological background upon which management must be based and focus on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, they discuss and evaluate management recommendations currently in use or proposed elsewhere.

Scope

The Brewer's sparrow conservation assessment examines the biology, ecology, conservation, and management of this species with specific reference to the geographic and ecological characteristics of the USFS Region 2. This document incorporates literature originating from field investigations within and outside of this region, placing the latter into the ecological and social contexts of the Rocky Mountain Region. The assessment focuses on biology and ecology of the Brewer's sparrow in the context of the current environment, but with consideration of its evolutionary environment.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on Brewer's sparrows were used in the assessment, nor were all published materials considered equally reliable. This assessment emphasizes refereed literature because it is the accepted standard in science. Non-refereed publications or reports were used when refereed information was unavailable elsewhere, but these were regarded with greater skepticism. These data sources required special attention because of the diversity of persons and methods used in data collection.

Treatment of Uncertainty

Science represents a rigorous, systematic approach to obtaining knowledge. Competing ideas regarding how the world works are measured against observations. However, because our descriptions of the world are always incomplete and our observations are limited, science focuses on approaches for dealing with uncertainty. A commonly accepted approach to science is based on a progression of critical experiments to develop strong inference (Platt 1964). However, it is difficult to conduct experiments that produce clean results in the ecological sciences. Often, we must rely on observations, inference, good thinking, and models to guide our understanding of ecological relations. In this assessment, we note the strength of evidence for particular ideas, and we describe alternative explanations where appropriate.

Publication of Assessment on the World Wide Web

To facilitate their use species conservation assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency personnel and the public more rapidly than publishing them as reports. More importantly, Web publication facilitates their revision, which will be accomplished based on guidelines established by Region 2.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, using at least two recognized experts on this or related taxa. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

Special management status of this species on USFS lands and states within Region 2.

❖ **Migratory Bird Treaty Act:** species is protected from "take" (U.S. Department of Interior 2002c).

❖ **U.S. Fish and Wildlife Service (USFWS) Birds of Conservation Concern:** species is considered a bird of conservation concern throughout its breeding and wintering ranges (ranked nationally, in USFWS Regions 1 and 6, and in all Bird Conservation Regions where it occurs) (U.S. Department of Interior 2002a).

❖ **USFS Rocky Mountain Region:** species is designated as a sensitive species (U.S. Department of Agriculture 2003) and as an MIS on three National Forest System units (Shoshone, Bighorn, White River national forests).

❖ **Bureau of Land Management (BLM):** species is listed as sensitive in all counties of Wyoming (U.S. Department of Interior 2002b).

❖ **National Audubon Society:** species is considered a yellow Watchlist species (species is declining but at a slower rate than those in the red category. These typically are species of national conservation concern) (National Audubon Society 2002a).

❖ **Natural Heritage Program (NHP) Conservation Status:** global rank of G5 (secure).

❖ **State Heritage Program Conservation Status:**
   ✧ *Colorado Natural Heritage Program (2002):* species is not ranked.
   ✧ *South Dakota Natural Heritage Program:* species is ranked S2B (imperiled because of rarity in the state during breeding season or because of some factor(s) making it especially vulnerable to extinction) (www.natureserve.org).
   ✧ *Kansas Natural Heritage Inventory:* species is ranked S1B (critically imperiled in state because of extreme rarity during breeding season or because of some factor(s) making it especially vulnerable to extirpation from the state) (www.natureserve.org).
   ✧ *Wyoming Natural Diversity Database:* species is not listed as a species of concern (www.natureserve.org).
   ✧ *Nebraska Natural Heritage Program:* species is not listed as a species of concern (www.natureserve.org).

❖ **Partners in Flight (PIF) Bird Conservation Plans:**
   ✧ *Colorado Land Bird Conservation Plan (Biedleman 2000):* Priority Species for Colorado Plateau and the Southern Rocky Mountain Physiographic Areas in the Priority Habitat Sagebrush Shrubland.
   ✧ *Wyoming Bird Conservation Plan (Cerovski et al. 2001):* Level I (Conservation Action) Species in two of Wyoming's Highest Priority Habitats: Shrub-steppe and Mountain-foothills Shrub.
   ✧ *Wyoming Basin Physiographic Area:* Brewer's sparrow and Shrubsteppe habitat are a Priority Species and Priority Habitat.

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Currently, the Brewer's sparrow is protected under the Migratory Bird Treaty Act of 1918, which prohibits "take" of migratory birds unless permitted by regulations. Take is defined by the Act to mean "hunt, take, capture, offer for sale, offer to purchase, export, at any time, or in any manner, including any part, nest, or egg of any such bird." (16 U.S.C. 703).

USFS Region 2 lists the Brewer's sparrow as a sensitive species. Conservation strategies are to be developed and implemented for sensitive species and their habitats, in coordination with other National Forest System units, managing agencies, and landowners. Region 2 will coordinate management objectives to conserve sensitive species with state and federal agencies and other cooperators as appropriate. Approaches may include collaboratively developing individual species or multi-species conservation strategies, formalizing interagency conservation agreements, and incorporating recommendations into management direction set forth in Land and Resource Management Plans. Scientific information, including Regional species evaluations, species and ecosystem assessments, and conservation strategies, are to be integrated into USFS planning and implementation. Additionally, appropriate inventories and monitoring of sensitive species are to be conducted to improve our knowledge of the species' distribution, status, and responses to management activities, coordinating efforts within the Region and with other agencies and partners where feasible (U.S. Department of Agriculture 2003).

Under the National Forest Management Act the USFS is required to sustain habitats that support healthy populations of native and desired non-native plant and animal species on national forests and grasslands. Legally

required activities include monitoring population trends of MIS in relationship to habitat change, measuring the effects of management practices, monitoring the effects of off-road vehicles, and maintaining biological diversity. The standards and guidelines of the Forest Service Government Performance Results Act ensure that resources are managed in a sustainable manner. The National Environmental Policy Act requires agencies to specify environmentally preferable alternatives in land use management planning. Additional laws with which USFS management plans must comply are the Endangered Species, Clean Water, Clean Air, Mineral Leasing, Federal Onshore Oil and Gas Leasing Reform, and Mining and Minerals Policy acts; all are potentially relevant to Brewer's sparrow conservation.

The BLM is developing major programs for restoration of sagebrush ecosystems throughout the western United States (Paige and Ritter 1999, Beever and Pyke 2002, U.S. Department of Interior 2002d). These areas include important habitat for Brewer's sparrows, especially those areas of extensive sagebrush habitat with shrubs occurring in tall, clumped, and vigorous stands.

Declines in numerous bird populations have led to concern for the future of migratory and resident bird species. In 1990, the National Fish and Wildlife Foundation brought together federal, state, and local government agencies, private foundations, conservation groups, industry and the academic community to form a program to address the problem. Thus, Partners in Flight (PIF) was conceived as a voluntary, international coalition dedicated to "keeping common birds common" and "reversing the downward trends of declining species." Landbird conservation plans have been or are being developed for each state and/or physiographic region (modified from original strata devised by the Breeding Bird Survey) (Robbins et al. 1986). These Bird Conservation Plans form the foundation for PIF's long-term strategy for bird conservation. They identify priority species and habitats and establish objectives for conserving and monitoring bird populations and their habitats. Although priorities and biological objectives are identified at the physiographic area level, implementation of PIF objectives is meant to take place at different scales, including individual states, federal agency regions, joint ventures, and Bird Conservation Regions (BCRs). These plans have identified the Brewer's sparrow and its habitats within USFS Region 2 as priorities for conservation.

The states within USFS Region 2 that have completed PIF Bird Conservation Plans are Colorado and Wyoming. The Colorado Land Bird Conservation Plan (Biedleman 2000) lists the Brewer's sparrow as a Priority Species for 1) the Colorado Plateau Physiographic Area in the Priority Habitat Sagebrush Shrubland and 2) the Southern Rocky Mountain Physiographic Area in the Priority Habitat Sagebrush Shrubland. Likewise, the Wyoming Bird Conservation Plan (Cerovski et al. 2001) lists the Brewer's sparrow as a Level I (Conservation Action) species for two of Wyoming's Highest Priority Habitats: Shrub-steppe and Mountain-foothills Shrub. The Physiographic Areas within Region 2 include Central Rocky Mountains (No. 64), Southern Rocky Mountains (No. 62), Colorado Plateau (No. 87), Wyoming Basin (No. 86), Northern Shortgrass Prairie (No. 39), Central Shortgrass Prairie (No. 36), West River (No. 38), and Central Mixed-grass Prairie (No. 34). Of these, the Wyoming Basin Plan lists Brewer's sparrow and Shrubsteppe habitat as a Priority Species and a Priority Habitat, respectively.

The Land Bird Conservation Plan for Colorado (Biedleman 2000) contains Implementation Strategies for conserving priority species and habitats. For Brewer's sparrows and their associated habitat of Sagebrush Shrubland, the Plan calls for monitoring Brewer's sparrows to document distribution, population trends, and abundance. They propose using BBS data and incorporating Monitoring Colorado Bird (MCB) data as it becomes available. MCB was implemented in sagebrush habitat in 1999; currently no results of this monitoring have been published. The plan also proposes to document the amount, condition, and ownership of sagebrush habitat in Colorado and to conserve unique representatives and/or large, ecologically-functioning examples of sagebrush habitat in Colorado. While these efforts have not been initiated, the Colorado Division of Wildlife is working on a range-wide conservation plan for the Gunnison sage grouse (*Centrocercus minimus*), a species that may use habitat in a similar way to the Brewer's sparrow and/or respond similarly to threats, management, and conservation activities (Biedleman 2000).

Both the Colorado and Wyoming Bird Conservation Plans propose implementing a list of "Best Management Practices" for shrublands to benefit birds. These are excerpted from "Birds in a Sagebrush Sea" (Paige and Ritter 1999) and are detailed in the section on "Potential Management." These practices have not yet been implemented by federal or state agencies. There is no information on the extent to which private entities are implementing these management practices.

The Brewer's sparrow is listed as critically imperiled in Kansas (www.natureserve.org), but the

state has not established management or conservation goals for the species. Currently, programs under the Kansas Department of Wildlife and Parks or Kansas Natural Heritage Inventory do not have conservation or restoration objectives for sagebrush ecosystems, where Brewer's sparrows occur. However, management and conservation plans are currently being developed and should be available in the near future (Kansas Department of Wildlife and Parks 2004 personal communication). The only current plans in Kansas that apply to sagebrush conservation are the Nature Conservancy Ecoregional Plans (The Nature Conservancy 2000).

Currently, no programs under the Nebraska Game and Parks Department or the Nebraska Natural Heritage Program have conservation or restoration objectives for sagebrush ecosystems or Brewer's sparrows. However, management and conservation plans are currently being developed by the Game and Parks Department and should be available in the near future (Nebraska Game and Parks Department 2004 personal communication). The only current plans in the state of Nebraska that apply to sagebrush conservation are the Nature Conservancy Ecoregional Plans (The Nature Conservancy 2000).

The South Dakota Natural Heritage Program lists Brewer's sparrow as imperiled, but the state has not established management or conservation goals for this species. No programs under the South Dakota Game, Fish and Parks Department and South Dakota Wildlife Diversity Program contain conservation or restoration objectives for sagebrush ecosystems where Brewer's sparrows occur in South Dakota. However, management and conservation plans are currently being developed and should be available in the near future (South Dakota Game, Fish, and Parks Department 2004 personal communication). The only plans in South Dakota that apply to sagebrush conservation are the Nature Conservancy Ecoregional Plans (The Nature Conservancy 2000).

State and federal management agencies have the capability to conduct the actions needed to conserve sagebrush ecosystems as an integral part of their larger missions. These agencies have identified the importance of birds and habitats in sagebrush ecosystems. However, the resources currently spent on shrubland birds fall far short of what is necessary to adequately address the issues facing these ecosystems and the birds dependent on them. Development of a comprehensive approach to bird conservation in sagebrush habitats requires a broad range of partnerships, which should include state and federal agencies, academia, and private organizations.

Adequacy of laws and regulations to conserve the species

The existing regulatory mechanisms, management plans, and conservation strategies described above may be adequate to protect the species. Yet, political will and public support is needed to fully implement these policies and strategies and to effectively conserve this species and its habitats. The processes that destroy, fragment, and degrade sagebrush shrubsteppe continue to affect virtually all sagebrush habitats and have led to the current situation where the bird species perhaps most in need of conservation attention are those most typical of undisturbed shrub steppe, including the Brewer's sparrow (Rotenberry 1998).

There are a number of management practices currently employed within the species' range that are clearly inadequate to conserve Brewer's sparrow populations or sagebrush shrublands. The following management practices can have detrimental effects on the conservation of this species and its habitat.

1. Improper management of livestock can result in changes to native ecosystems including invasion of non-native species and alteration of fire regimes (as occurs with invasion by annual brome grasses). Historical heavy livestock grazing has altered much of the sagebrush range, changing plant composition and densities (Saab et al. 1995). In some cases, changes in water and nutrient cycling caused by grazing can promote the spread of invasive species, which can then degrade habitat for native bird species by altering fire and disturbance regimes (Rotenberry 1998). For the most part, USFS Region 2 lands have not suffered from altered fire regimes due to invasive annual plants (C. Quimby 2004 personal communication).

2. There is uniform agreement that fire frequencies in the Intermountain West have been altered greatly over the past 150 years (Dobkin and Sauder 2004). In some areas, as a result of fire suppression and the loss of fine fuels to grazing, fire-return intervals are now much longer. In other places, fire-return intervals are dramatically shorter due to the spread and dominance of fire-promoting exotic species (Dobkin and Sauder 2004). Fire kills sagebrush, and where non-native grasses dominate, the landscape can be converted to annual grassland as the fire

cycle becomes shorter, removing preferred habitat (Paige and Ritter 1998). These effects have not been severe in Region 2 (C. Quimby 2004 personal communication), but they have affected much of the species' habitat outside the region.

3. Management practices that result in disturbance of shrubland sites, such as manipulation of sagebrush to increase forage for livestock, and road development for energy production, promote the invasion of exotic grasses, such as cheatgrass, that have come to dominate the grass-forb community of more than half the sagebrush region in the West, replacing native bunchgrasses (Rich 1996). Crested wheatgrass (*Agropyron cristatum*) and non-native annuals have fundamentally altered the grass-forb community in many areas of sagebrush shrubsteppe, altering shrubland habitats.

The ongoing threats to sagebrush ecosystems are numerous, and their consequences will require long and expensive recovery; in some areas, they are largely irreversible (Rotenberry 1998, Knick 1999, Knick et al. 2003). In the absence of active restoration, exotic grasses will continue to invade and degrade the quality of sagebrush landscapes (Wisdom et al. 2000). Aggressive management actions (e.g., removal of cheatgrass and the factors that promote it) might stabilize current conditions (Knick et al. 2003). However, declines in habitat condition and extent were projected outcomes of most management scenarios in sagebrush habitats in the Interior Columbia River Basin (Raphael et al. 2001, Wisdom et al. 2002, Knick et al. 2003).

Enforcement of existing laws and regulations

Protection from use is not a viable option for sagebrush lands. Very little of the geographic distribution of the Brewer's sparrow's habitat has protected status in the form of national parks, USFS and BLM wilderness areas, or national wildlife refuges (Scott et al. 2001, Wright et al. 2001). For example, less than 2 percent of the sagebrush lands in the Columbia Plateau and 3 percent in the Great Basin are within national parks or Departments of Energy or Defense reserves. However, even these reserves do not necessarily provide protection from management practices that may be detrimental to the Brewer's sparrow and its habitat. For instance, BLM-designated wilderness areas are managed for grazing and other uses (U.S. Department of Interior

2002d). Purchasing lands for protection (Shaffer et al. 2002) is not feasible because the areas likely required to maintain intact sagebrush ecosystems are too large and costly. Rather, enforcement of sound management policies based on an understanding of the effects of land use practice may be the only way to ensure long-term survival of sagebrush ecosystems and their associated avifauna (Knick et al. 2003).

Approximately two-thirds of the total area occupied by sagebrush in the western United States is managed by federal government agencies, primarily the BLM (Knick et al. 2003, Dobkin and Sauder 2004). Therefore, responsibility for maintaining sagebrush habitats and their associated avifauna rests on public land management policies. Because many of the birds breeding in sagebrush ecosystems (e.g., Brewer's sparrow, sage sparrow [*Amphispiza belli*]) are short-distance migrants, the issues are largely contained within the United States. The primary challenge is to respect the intrinsic value of sagebrush ecosystems and its unique biodiversity (Knick et al. 2003).

Biology and Ecology

Systematics and general species description

There are two recognized subspecies, or allospecies, of Brewer's sparrow (*Spizella breweri*): the Brewers' sparrow (*S. b. breweri* Cassin 1856) and the timberline sparrow (*S. b. taverneri* Swarth and Brookes 1925). The timberline sparrow was originally described as a separate species, and it is still recognized as such by some authorities (Sibley and Monroe 1990, Rotenberry et al. 1999). These subspecies differ in morphology, song, breeding habitat, and geographic range (Swarth and Brooks 1925, Oberholser 1974, Pyle and Howell 1996, Doyle 1997, Rotenberry et al. 1999).

Brewer's sparrows are typical *Spizella* sparrows, being small, slim, and long-tailed, with a thin conical bill and a notched tail. There is a slight sexual size dimorphism; otherwise both genders look alike.

The timberline sparrow differs morphologically from the nominate *breweri* in having a darker and grayer coloration, with a stronger contrast between the gray breast and the white abdomen. Additionally, the streaking on the back is heavier and coarser, and the head patterns are bolder. There is a greater tendency toward narrow streaking on the flanks, and the nape is more heavily streaked. Overall, the timberline sparrow is larger, with a smaller, more slender, and

more extensively dark bill. These differences are subtle, and field identification of the timberline sparrow is problematic (Rotenberry et al. 1999).

The Brewer's sparrow has two song types: a short song comprised of one to three buzzy-sounding trills and a long song that has five to ten trills. Only the male is known to sing; both genders produce a weak call note of "tsip", "chip", or "seep" (Rotenberry et al. 1999).

Distribution and abundance

Current and historic global distribution

The Brewer's sparrow (*Spizella breweri breweri*) is concentrated in the Great Basin from the eastern half of Washington and southern British Columbia to southwestern Saskatchewan (Smith 1996), and most of Montana, except portions of the northwest and northeast of the state. It is also found in the southern sections of Idaho through eastern Oregon, eastern California, and the northern sections of the Mojave Desert (Small 1994). This subspecies extends through all of Nevada, Utah, Wyoming, northern Arizona, northwestern New Mexico, and western, central, and eastern Colorado (Hubbard 1978, Andrews and Righter 1992, Bergeron et al. 1992, Gilligan et al. 1994, Small 1994, Arizona Breeding Bird Atlas unpublished). It breeds regularly

in southwestern North Dakota to southwestern South Dakota, and extreme northwestern Nebraska, with an isolated population in extreme southwestern Kansas (Stewart 1975, Johnsgard 1979, Thompson and Ely 1992). Brewer's sparrows also breed sporadically eastward to Oklahoma, central Nebraska, and the Texas Panhandle (Johnsgard 1979). It is an uncommon breeder in southern California (Small 1994, Rotenberry et al. 1999). The current distribution of Brewer's sparrows is assumed to be similar to the historical (Dobkin and Sauder 2004). The regional distribution of abundances for the Brewer's sparrow based on Breeding Bird Survey data, is shown in **Figure 2**.

The breeding range of the timberline sparrow includes two widely separated areas. It breeds in the mountains of extreme southwestern Alberta and probably in the adjacent mountains of extreme southeastern British Columbia. It also breeds from extreme northwestern British Columbia, northwest through southwestern Yukon. There are also small populations in southeastern Alaska (Rotenberry et al. 1999).

The winter range of both subspecies extends from southeastern California, central Arizona, southern New Mexico, and western Texas (Oberholser 1974, Hubbard 1978, Monson and Phillips 1981, Small 1994). In
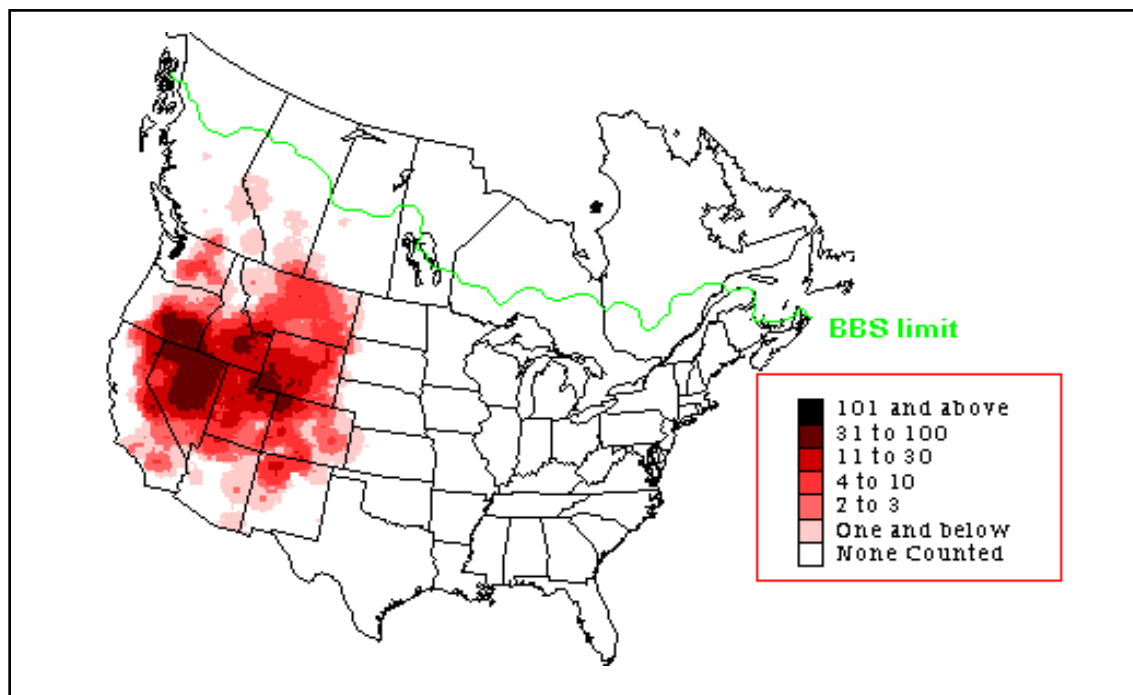

Figure 2. Relative breeding season abundance (average number of birds per route) of the Brewer's sparrow based on Breeding Bird Survey data from 1982 to 1996 (Sauer et al. 2003).

Mexico, the Brewer's sparrow is known to winter in Baja California, Sonora, and through the highlands of northern Mexico from eastern Chihuahua, Coahuila and western Nuevo Leon to northern Jalisco and Guanajuato (Howell and Webb 1995, Rotenberry et al. 1999). Winter Brewer's sparrow distribution based on Christmas Bird Counts is shown in **Figure 3**.

Regional current and historic distribution and abundance

Within Region 2, the Brewer's sparrow breeds in western, central, and portions of eastern Colorado (**Figure 4**; Andrews and Righter 1992, Lambeth 1998). In Kansas, territorial males have been observed in Morton County (Johnsgard 1979). Thompson and Ely (1992) have breeding records for Morton and Finney counties, in southwestern Kansas. Two additional non-breeding bird atlas records are in Morton and Stevens counties in the southwestern section of the state (Thompson and Ely 1992). In Nebraska, the Brewer's sparrow breeds in the northwestern part of the state; it has been confirmed to breed in Sioux County, and there is one record in Howard County (Johnsgard 1979). It also breeds locally along the extreme northwestern and southwestern edges of South Dakota, excluding the Black Hills (**Figure 5**; Peterson 1995, Johnsgard 1979). It breeds throughout Wyoming (Rotenberry et al. 1999).

Breeding-season surveys have found that Brewer's sparrows are often the most abundant species on their nesting grounds. In some areas they can reach densities of 150 to 300 birds per km^2 and can exceed 500 birds per km^2 in some locations (Reynolds 1981, Rotenberry and Wiens 1989). Based on plot counts in Montana, densities were about 200 individuals per km^2 (n = 5 plots; Best 1972). In southeastern Idaho, there were 116 to 192 individuals per km^2 (n = 4 plots, sampled for 4 to 8 years; Petersen and Best 1987). In central Oregon, densities ranged from 111 to 277 individuals per km^2 (n = 2 plots, sampled for 8 years; J. T. Rotenberry and J. A. Wiens unpublished data cited in Rotenberry et al. 1999). Other breeding sites sampled in Oregon averaged 200 individuals per km^2 over three years, ranging from 29 to 533 individuals per km^2 (Rotenberry and Wiens 1980a). Densities can be highly variable; one site was unoccupied during one year, and then attained densities of 150 individuals per km^2 the next year (Rotenberry et al. 1999). In a comparison of BBS data from 1968 to 1983 and data from 1984 to 2001, many BBS routes with reduced abundances of Brewer's sparrow were located at the periphery of the species' distribution (Dobkin and Sauder 2004), including much of eastern

Wyoming and Colorado (Kansas, Nebraska, and South Dakota were not included in the analysis).

Discontinuities in distribution and degree of isolation of populations

Breeding populations of the Brewer's sparrow appear mostly contiguously distributed, although relative abundance differs across the species' range. Two centers of abundance, in eastern Washington and in northwestern New Mexico, are slightly disjunct from the species' main distribution (Rotenberry et al. 1999).

Population trend

North American Breeding Bird Survey (reference period 1966 to 2002)

Breeding Bird Surveys (BBS) were designed to provide a continent-wide perspective of population change. These surveys produce an index of relative abundance rather than a complete count of breeding bird populations. The data analysis assumes that fluctuations in these indices of abundance are representative of the population as a whole (Sauer et al. 2001). However, these data should be viewed with some caution. Local trends are sometimes difficult to interpret and can be quite different from larger-scale BBS trends (Peterjohn 1989).

Breeding Bird Surveys are conducted throughout North America during the peak of the breeding season, primarily in May and June, earlier in desert regions and some southern states where the breeding season begins earlier. Each route is 24.5 miles long with a total of 50 point count stations located at 0.5-mile intervals along the route.

BBS data for Brewer's sparrows at the continental (survey-wide), western regional, and central regional scales indicate significant declining trends in relative abundance between 1966 and 2002, ranging from -2.75 percent per year in the western region to -3.8 percent per year in the central region. When the time period is portioned, these regions also show decreases (**Table 1**). No physiographic region had a significant increasing trend in Brewer's sparrow relative abundance. The relative abundance indices among the levels of data presented appear to accurately represent Brewer's sparrows where they are abundant within Region 2, and the negative trends appear to be consistent throughout the 30-year survey period. Despite the limitations of BBS data to accurately track sparrow population trends at anything other than at gross geographic scales and
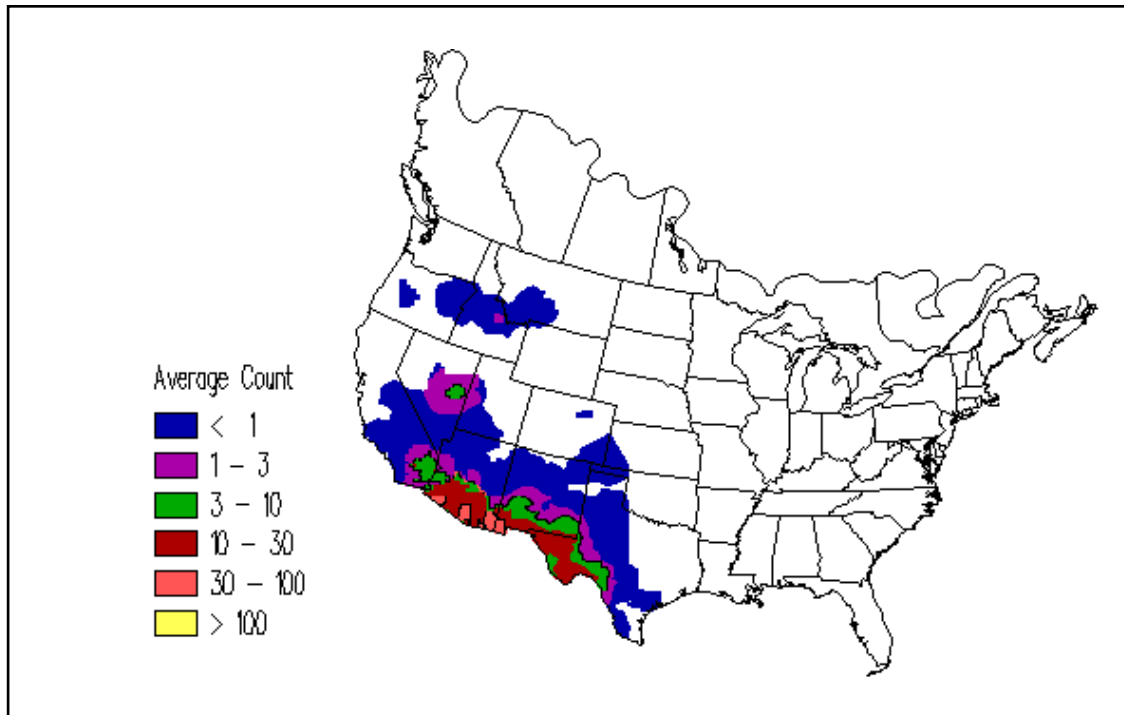
Figure 3. Winter season distribution and relative abundance of the Brewer's sparrow based on Christmas Bird Counts data from 1959 to 2003 Sauer et al. 1996b).
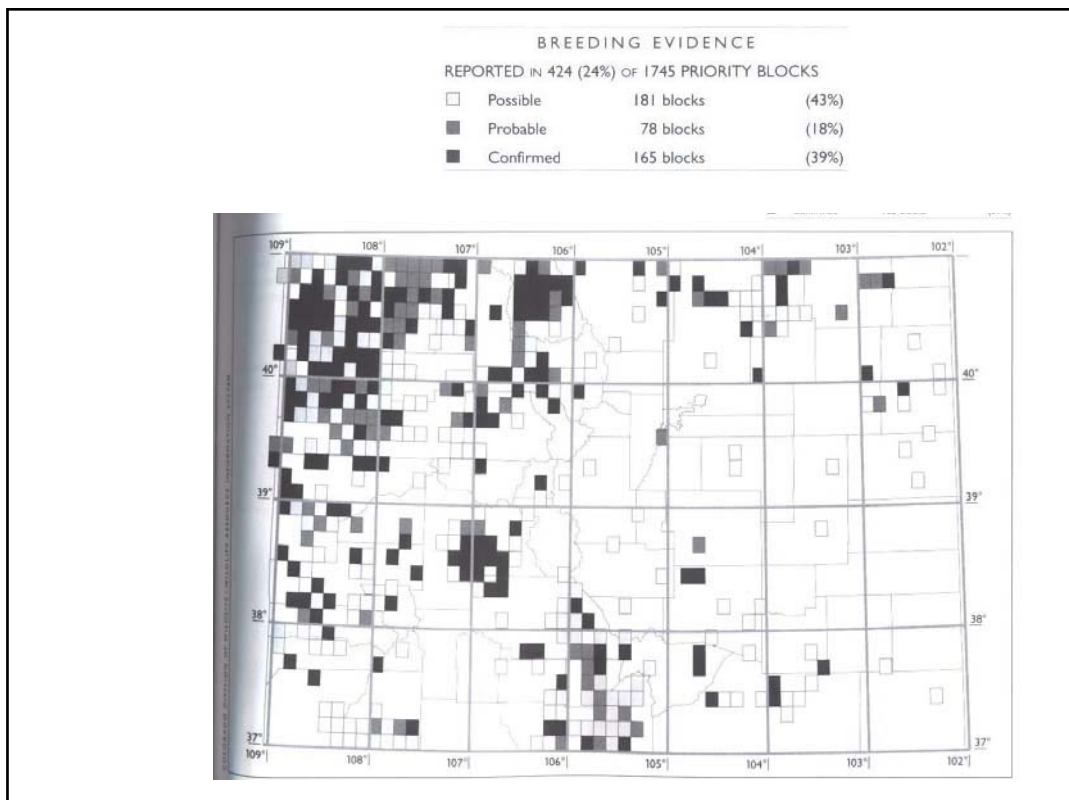
Figure 4. Brewer's sparrow detections during the Colorado Breeding Bird Atlas Project (Kingery 1998).
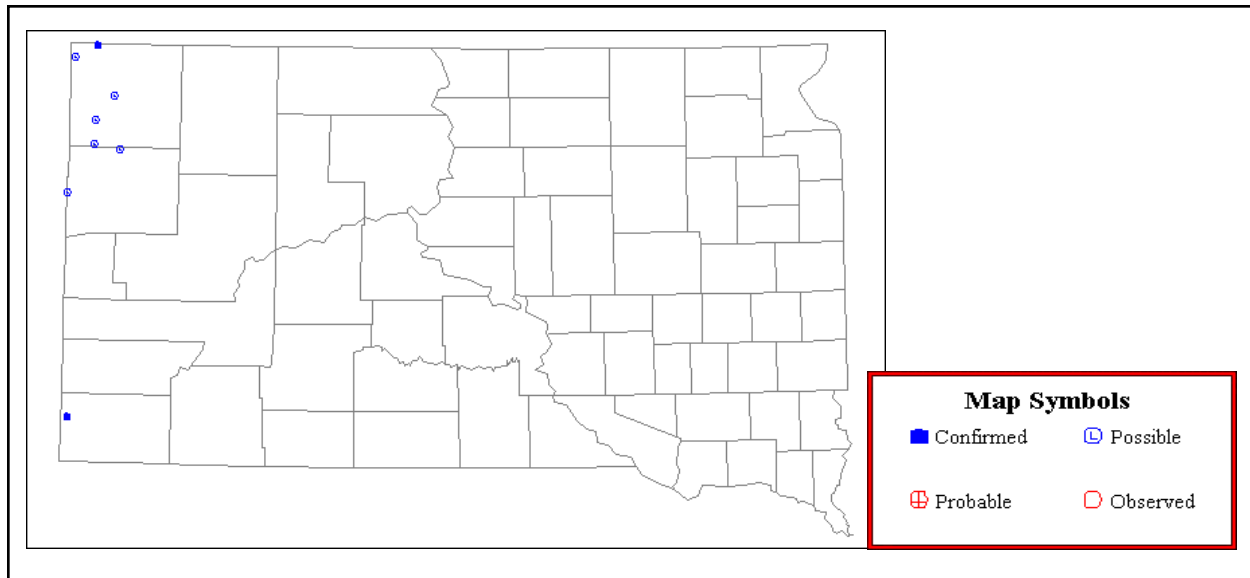
Figure 5. Map of South Dakota Breeding Bird Atlas Brewer's sparrow detections (Peterson 1995).

Table 1. Breeding Bird Survey trend data for the Brewer's sparrow from 1966 to 2002 (From Sauer et al. 2004).

	1966-2002			1966-1979			1980-2002		
Location	Trend	*P* value	N	Trend	*P* value	N	Trend	*P* value	N
United States	-2.9	0.00	463	-2.2	0.13	125	-2.3	0.00	441
Western Region	-2.7	0.00	395	-2.0	0.25	106	-2.3	0.00	378
Central Region	-3.8	0.01	80	-2.5	0.43	20	-1.9	0.20	75
Wyoming Basin	-0.7	0.46	50	-1.8	0.69	13	-0.5	0.64	50
Great Basin	0.8	0.70	23	17.6	0.35	6	0.0	0.98	21
Southern Rockies	-0.17	0.94	32	18.42	0.41	3	1.2	0.71	32
Colorado	-3.3	0.00	69	-9.43	0.47	15	-2.0	0.11	66
Wyoming	-1.5	0.07	96	-3.88	0.00	22	-0.5	0.63	93
Kansas	a	a	a	a	a	a	a	a	a
Nebraska	-13.0	0.56	2	a	a	a	a	a	a
South Dakota	-1.4	0.79	3	a	a	a	-1.4	0.83	3

a = No data.

over long time intervals, it appears from these data that Brewer's sparrow populations are declining throughout much of Region 2 (**Table 1**; **Figure 6**).

Colorado trends

Although Brewer's sparrows are considered common in western Colorado (Andrews and Righter 1992), trend estimates show significant decreases from 1966 to 2002 (**Table 1**; Sauer et al. 2004). Declines are most pronounced between 1966 and 1979. In an analysis of detection frequencies on BBS routes that compared detection frequencies for the periods 1968 to 1983 and 1984 to 2001 (Dobkin and Sauder 2004),

detection frequencies on routes in western, southern, and eastern Colorado declined, while in north-central Colorado they increased.

Wyoming trends

Within Wyoming, trend estimates show non-significant decreases between 1966 and 1979 and between 1980 and 2002. Declines are more pronounced between 1966 and 1979 than between 1980 and 2002 (**Table 1**). The average number of Brewer's sparrows per route between 1966 and 2002 was 17.7, with highest abundances found in the southwestern part of the state (Sauer et al. 1996a). In an analysis of detection
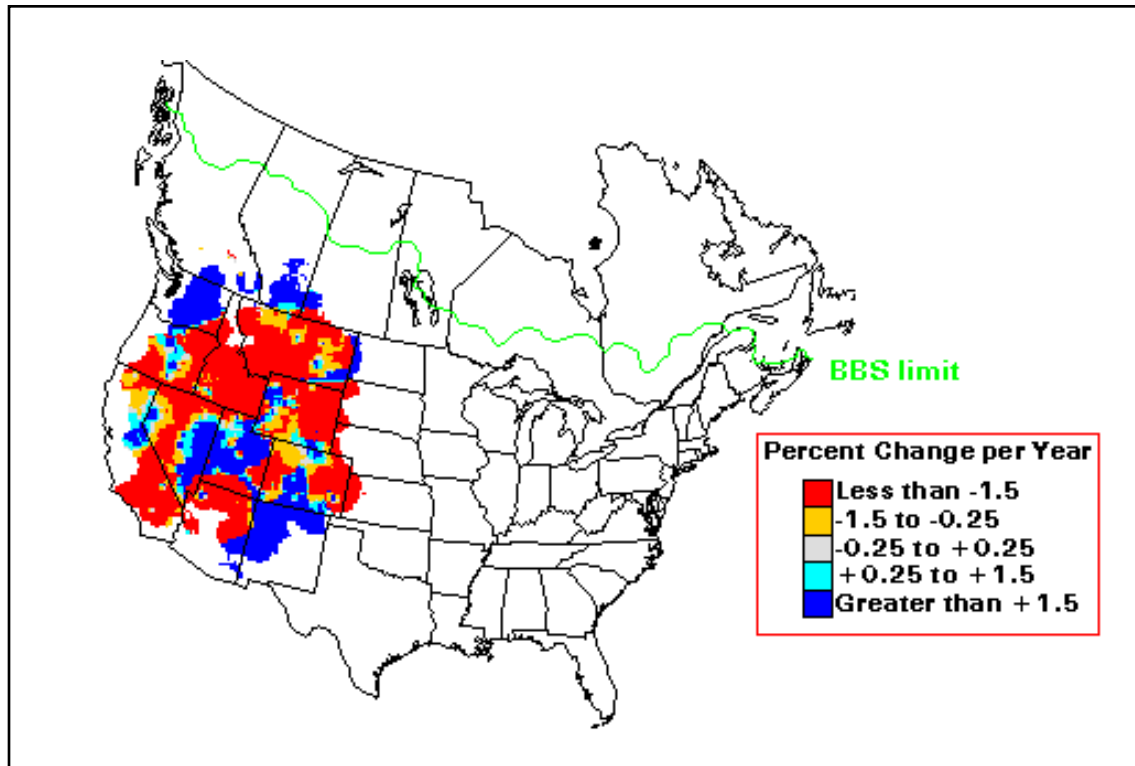
Figure 6. Brewer's sparrow trends (average percent population change per year) based on Breeding Bird Survey data from 1966 to 2002 (Sauer et al. 2003).

frequencies on BBS routes for the periods 1968 to 1983 and 1984 to 2001 (Dobkin and Sauder 2004), detection frequencies on routes in the southern half of the state and in eastern Wyoming declined, while those in northwestern Wyoming and the extreme southwestern corner of the state increased.

South Dakota trends

BBS data show a non-significant increase between 1966 and 2002, but a non-significant decrease for the period 1980 through 2002. Over the entire time period, the average number of Brewer's sparrows per route was 0.06.

Kansas and Nebraska trends

BBS data for Kansas and Nebraska were insufficient to provide trend estimates.

Winter counts

BBS winter counts show the highest winter abundance within the United States in southern Arizona, New Mexico, and western Texas. There is no information on abundance in Mexico (Sauer et al. 1997, Rotenberry et al. 1999).

Mapped Christmas Bird Count (CBC) data show highest United States abundance in the borderlands of southern Arizona, southern New Mexico, and western Texas (Sauer et al. 1996b). CBC data for the United States for the period from 1959 to 1988 indicate a stable, though non-significant, survey-wide increasing trend (0.2 percent average annual increase, $p > 0.10$, $n = 116$), and a significant increase (6.7 percent average annual increase, $p < 0.01$, $n = 33$) in Texas (Sauer et al. 1996b). Counts from CBC have high annual variation, and the end date used to calculate the Texas trend (i.e., 1988) represents a peak in the number of Brewer's sparrows per party hour. The positive trend appears to be a consequence of the end dates selected for the period analyzed. Data from the period 1988 to 2003 also show high variability from year to year, with the number observed per party hour in 2003 nearly the same as that in 1959 (National Audubon Society 2002b). Estimates from CBC data are not comparable to those from BBS data for several reasons:

❖ high variability in winter count data

❖ different sampling methods

- ❖ the majority (104 of 116) of CBC trend analysis routes are located outside or on the periphery of the Brewer's sparrow's breeding range

- ❖ Brewer's sparrow requirements in wintering areas are likely different form those on their breeding grounds

- ❖ threats being experienced on wintering areas are different from those on breeding grounds

- ❖ CBC routes cover only a portion of the Brewer's sparrow's wintering range within the United States.

Activity pattern and movements

Circadian, Seasonal, Circannual

No formal daily (circadian) time budgets have been reported (Rotenberry et al. 1999). Wiens et al. (1987b) made periodic behavioral observations of male Brewer's sparrows (with sample sizes varying from 120 to 585) on their breeding grounds and found that in 60 percent of the observation periods males were singing; in 44 percent, individuals were foraging; in 24 percent, they were preening or inactive; in 21 percent they were in flight; and 16 percent of the observation periods involved aggression. The proportions do not sum to 100 because observation periods during which an activity did not occur were omitted (Rotenberry et al. 1999). Brewer's sparrows intersperse singing with foraging within bouts of foraging (Wiens et al. 1990), and songs tend to be delivered from widely spaced perches (Rotenberry et al. 1999). The proportion of time males spent singing on the breeding grounds varied from 0.44 to 0.65 (averaged over 600 observation periods, 4 years, 2 plots; Wiens et al. 1987b, Rotenberry et al. 1999).

Brewer's sparrows are a nearctic-neotropical migrant and thus have a circannual activity pattern in which they are an early spring migrant. Males arrive on the breeding grounds several days before females and begin to establish territories. The timing of territory establishment and pair formation may depend on average temperatures in late April; these were later following colder temperatures (Best and Petersen 1985). The nesting season of the Brewer's sparrow extends from mid-April to early August, with most nesting activity concentrated between mid-May and late July (Rotenberry et al. 1999). The extent to which individuals move locally (i.e., nomadism) in the

time period between post-breeding and migration is unknown (Rotenberry et al. 1999).

Juvenile plumage is generally retained between June and August (Pyle et al. 1987, Rotenberry et al. 1999). Post-juvenile molt (Prebasic I) is partial and begun on the breeding grounds, soon after fledging, interrupted during migration, and resumed on the wintering grounds (Rotenberry et al. 1999). Adult post-breeding (Definitive Prebasic) molt is complete and generally occurs on the breeding ground between approximately 3 July and 27 October. A pre-breeding season molt is partial to incomplete and occurs between 1 March and 29 May (Rotenberry et al. 1999).

Fall migration takes place from mid-August through October. The northernmost populations begin migrating in August, and all individuals are gone by late September (Semechuck 1992, Rotenberry et al. 1999).

Brewer's sparrow daily activity patterns on wintering areas are not recorded. They are found in mixed-species flocks, frequently with other *Spizella* and other sparrows (Rotenberry et al. 1999).

Broad scale movement patterns

The majority of Brewer's sparrows breed in the Great Basin and winter in the Sonoran and Chihuahuan deserts of the southwestern United States, western Mexico, and the Mexican Plateau (Rappole et al. 1993, Rotenberry et al. 1999). The primary migratory route is through the intermountain west (Rotenberry et al. 1999), but actual migration pathways are unknown (Knick et al. 2003). Brewer's sparrows are rarely encountered east to western Kansas and the Okalahoma panhandle (Rising 1996, Rotenberry et al. 1999). Migration is nocturnal; data on orientation, altitude, and flight formation are not available. There are no data on winter site fidelity (Rotenberry et al. 1999), including yearly fidelity to winter areas (Knick et al. 2003) although Brewer's sparrows probably move farther south within their wintering range during below-average cold periods (Rotenberry et al. 1999).

Regional differences in migration and other broad scale movement patterns

The more northerly populations of Brewer's sparrows, *S. b. taverneri*, winter farther south than *S. b. breweri*, in an apparent leapfrog migration pattern (Rotenberry et al. 1999). In Alberta, *S. b. breweri* arrives in its northernmost breeding area (Alberta) in early

May, while *S .b. taverneri* arrives in late May (Paine 1968, Rotenberry et al. 1999). Peak migration periods for Brewer's sparrows in Nebraska occur around 5 May in the spring and during the first week of September in the fall (Faanes and Lingle 1995). In Colorado, Brewer's sparrows start to arrive in mid-April, with full numbers at the end of the month (Andrews and Righter 1992, Lambeth 1998).

Potential links to, or isolation from, other segments of the population; connectivity

The extent of dispersal and redistribution by individuals following migration and return to breeding areas is largely unknown. In southeastern Idaho about 25 percent of color-banded males returned to nesting areas used in the previous year (Petersen and Best 1987, Rotenberry et al. 1999), thus remaining within the same population.

Habitat

Macrohabitat

The Brewer's sparrow is an obligate of sagebrush communities (Braun et al. 1976, Paige and Ritter 1999). Throughout most of the Brewer's sparrow's breeding range it is most closely associated with landscapes dominated by big sagebrush (*Artemisia tridentata*) (Wiens and Rotenberry 1981a, Rotenberry et al. 1999) with an average canopy height of less than 1.5 m (Rotenberry et al. 1999). It also occurs in shrubby openings in pinyon-juniper (*Pinus edulus-Juniperus* spp.) and mountain mahogany (*Cercocarpus* spp.) woodlands (Sedgwick 1987) and large shrubby parklands within coniferous forests (Rotenberry et al. 1999). In northwestern Canada it is found at high elevations above timberline and in shrubby montane valleys dominated by low-growing willow (*Salix* spp.), dwarf birch (*Betula* spp.), and shrubs (Doyle 1997, Rotenberry et al. 1999).

While it is evident that the distribution of Brewer's sparrow is largely determined by the distribution of sagebrush, few studies have related distribution and abundance of shrubland birds to the composition and configuration of landscapes (Knick and Rotenberry 1995b, Vander Haegen et al. 2000, Knick and Rotenberry 2002). At a broad, regional scale, Brewer's sparrow abundances have been correlated with shrub cover (Wiens and Rotenberry 1980, 1981a). Density of singing males has been found to be greatest in unfragmented shrubland habitats (Knick and Rotenberry 1995b, 1999, 2002). Local densities

are negatively influenced by landscape-level habitat changes that increase fragmentation of shrublands and appear to be more sensitive to variation in landscape-level attributes than in local-scale habitat attributes (Rotenberry et al. 1999, Knick and Rotenberry 2000).

Landscape level attributes that are positively associated with Brewer's sparrow density include high shrub cover, large patch size, little fragmentation, low disturbance, and habitat heterogeneity (Knick and Rotenberry 1995b). Knick and Rotenberry (2002) found that the occurrence of Brewer's sparrows increased with increasing area of sagebrush patches and decreasing fragmentation. In the Snake River Birds of Prey National Conservation Area, they found that Brewer's sparrows were more likely to occur in sites with high shrub cover and large patch size and were associated with Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) communities (Knick and Rotenberry 2002). In Montana, Brewer's sparrows preferred sagebrush sites averaging 13 percent sagebrush cover (Bock and Bock 1987). The minimum patch size and the degree of patch isolation required for breeding have not been determined, but isolated stands of sagebrush smaller than 2 ha are not likely to be nesting habitat (Knick and Rotenberry 1995a).

Within Region 2, Brewer's sparrows are found across Wyoming in prairie and foothills sagebrush habitat (Cervoski et al. 2001). In Colorado, 75 percent of Brewer's sparrow detections were in sagebrush habitat (Lambeth 1998). In South Dakota, Nebraska, and Kansas, Brewer's sparrows are especially characteristic of prairies with sage or other semi-arid shrubs such as rabbitbrush (*Chrysothamnus* spp.) (Johnsgard 1979). In Kansas, small colonies were discovered in sand-sage (*Artemisia filifolia*) grassland (Thompson and Ely 1992), and they recently have been reported from the southwestern part of the state in areas containing sand-sage prairie (Busby and Zimmerman 2001). Studies examining the influence of landscape level habitat characteristics within Region 2 have not been conducted. It is likely that, within Region 2's sagebrush habitats, the amount of sagebrush cover, patch size, spatial distribution of patches, and the extent of disturbance and fragmentation influence Brewer's sparrow occupancy and abundance.

Microhabitat

Within its shrubland breeding habitat, local (e.g., within-patch) components that have been positively correlated with Brewer's sparrow densities are sagebrush cover, shrub cover, above-average vegetation

height, vigor of the shrub patch, and measures of horizontal habitat heterogeneity. Conversely, densities of Brewer's sparrows have been negatively correlated with grass cover, rock outcrops, hopsage (*Atriplex spinosa*) cover, saltbush (*A. canescens*) cover, budsage (*Artemisia spinescens*) cover, and shrub species diversity (Rotenberry and Wiens 1980a, Wiens and Rotenberry 1980, Wiens and Rotenberry 1981a, Larson and Bock 1984, Knopf et al. 1990, Paige and Ritter 1999). The negative correlation with grass cover indicates that they prefer areas dominated by shrubs compared to those dominated by grass (Paige and Ritter 1999). Densities of Brewer's sparrows were observed to decline on plots where the percent of sagebrush cover had been reduced through either experimental manipulation or wildfire (Bock and Bock 1987, Paige and Ritter 1999, Rotenberry et al. 1999). In other words, they tend to select healthy patches within a shrub community (Knopf et al. 1990).

Nest sites are located primarily in big sagebrush, in significantly taller, denser shrubs, with reduced bare ground and herbaceous cover when compared with the surrounding habitat (Petersen and Best 1985, Rotenberry et al. 1999). In Oregon and Nevada, 81 percent of 104 nests were built in big sagebrush, 10 percent were in spiny hopsage (*Grayia spinosa*), 6 percent were built in antelope bitterbrush (*Purshia tridentate*), and 3 percent were in green rabbitbrush (*Chrysothamnus viscidiflorus*) (Rotenberry et al. 1999). In Idaho, Brewer's sparrows used shrubs with a mean height of 69 cm for nesting; the average shrub height for the area was 43 cm. Seventy percent of the available shrubs were less than 50 cm tall, but only 7 percent of the nest shrubs were less than 50 cm tall (Petersen and Best 1985). Thus, Brewer's sparrows selected shrubs that had significantly greater mean height than shrubs in a representative sample of the habitat. Shrubs greater than 104 cm tall comprised only 1 percent of the available shrubs and were not used for nesting, possibly because of their spreading, open branch structure (Rotenberry et al. 1999). Other studies have found that the average Brewer's sparrow's nest shrub height was 66.9 cm in Idaho (Rich 1980); in Montana it ranged from 27.9 to 63.5 cm (Best 1972); in Oregon and Nevada the average height of nest shrubs was 71.4 cm (Rotenberry et al. 1999).

Brewer's sparrows prefer nest shrubs that are entirely alive or mostly alive (Petersen and Best 1985, Rotenberry et al. 1999). Although they select live shrubs with foliage, there is no preference among live shrubs for denser than average foliage (Rotenberry et al. 1999). Additionally, there is no preference for shrubs with discontinuous canopies (i.e., with gaps) versus continuous shrub canopies (Rotenberry et al. 1999). Knopf et al. (1990) found that they used shrubs with greater vigor (a higher proportion of live vegetation to dead vegetation) and hypothesized that the primary significance of shrub vigor as a habitat descriptor probably relates to its value as a predictor of food productivity (both insects and seeds) within a patch. In areas where all the shrubs were dead due to herbicide spraying, Brewer's sparrows used shrubs with dense branching and grass cover (Best 1972, Rotenberry et al. 1999).

The level of livestock grazing can also affect habitat use. In eastern Washington, Brewer's sparrow abundance was significantly lower at sites with poor range condition (less than 25 percent cover in climax vegetation) than at sites with fair condition (25 to 50 percent cover in climax vegetation), but abundance did not differ between fair and good sites (greater than 50 percent cover in climax vegetation).

During migration and in the winter, Brewer's sparrows are found in habitats similar to their breeding habitats. They are associated with sagebrush shrublands and brushy desert habitat, including desert scrub dominated by various saltbush species (*Atriplex* spp.) and creosote (*Larrea tridentata*) (Rotenberry et al. 1999).

Geographic distribution of habitat and change in extent over time

The majority of Brewer's sparrow habitat consists of the Intermountain shrubsteppe. This area historically consisted of large expanses of sagebrush and salt desert shrubs (primarily *Atriplex* spp.), with an understory of bunchgrasses and interspersed with grassland patches. Historic disturbance regimes (e.g., natural fire regimes, absence of livestock grazing) resulted in a mosaic of grasslands and different-aged patches of shrubland embedded within a larger shrub-dominated landscape (Knick and Rotenberry 2002). The sagebrush biome previously covered 63 million hectares (156 million acres) of western North America. Although the current geographic distribution of the sagebrush biome remains the same, very little remains undisturbed or unaltered from its condition prior to Euro-American settlement (West 1996, Dobkin and Sauder 2004).

Healthy shrubsteppe habitat has diminished greatly over the last 200 years (Dobkin and Sauder 2004). Human-caused impacts have contributed to extraordinary fragmentation and degradation across their widespread distribution (Knick et al. 2003, Dobkin

and Sauder 2004). Livestock grazing has affected 99 percent of the Intermountain sagebrush shrubsteppe, severely altering more than 30 percent. Additionally, these changes have altered the form and function of shrubsteppe regions throughout the Intermountain West by facilitating the spread of invasive plants, thus increasing the frequency and severity of disturbance (i.e., wildfire) and accelerating the fragmentation and loss of shrublands (Knick and Rotenberry 2002).

In Wyoming, the composition of sagebrush habitats has changed from historic conditions in that the grass species present today include exotics such as cheatgrass (Cervoski et al. 2001). Oil and gas wells have been located primarily in landscapes dominated by sagebrush, fragmenting these habitats (Knick et al. 2003).

Sagebrush in Colorado occurs at elevations of approximately 1,200 to 3,050 m (4,000 to 10,000 ft) and exists in a variety of climatic conditions, including low-elevation semi-desert habitats and moist, cool, mountainous areas. Perhaps 30 percent of Colorado's sagebrush was altered between 1900 and 1974 (Braun et al. 1976), and the ecological integrity of Colorado's sagebrush shrublands has been compromised by the invasion of exotic (e.g., cheatgrass) or native (e.g., pinyon-juniper) plant species, conversion to agricultural, residential, and other developed land types, and changes in natural fire regimes (Biedleman 2000).

In Nebraska it is estimated that the sand-sage prairie has been reduced by 50 percent from historic times (Teaming with Wildlife 2002). We could find no information regarding changes in the distribution of sagebrush habitats in South Dakota and Kansas. In general, these states have experienced considerable agricultural development and shrub removal related to livestock grazing since Euro-American settlement.

Habitat availability relative to occupied habitat

Although no studies specifically report on habitat occupied relative to that which is available, any given site may be unoccupied in one year, then attain densities of 150 individuals per km^2 the next (Rotenberry et al. 1999). This indicates a dynamic distribution pattern and that there may be more habitat available than is occupied during a given breeding season. The influences of patch dynamics, succession, and temporal effects on habitat availability and occupancy are unknown.

Food habits

The foraging behavior of the *breweri* race during the breeding season is well studied. It forages mostly in shrubs, and those shrubs selected are larger, more vigorous, and more likely to be sagebrush than green or gray rabbitbrush (Rotenberry and Wiens 1998, Rotenberry et al. 1999). They forage relatively little on open ground between shrubs or at the base of bunchgrasses (Wiens et al. 1987a, Rotenberry et al. 1999).

Primary food items during the breeding season are small insects gleaned mostly from the foliage and bark of shrubs or dwarf trees (Rotenberry et al. 1999). Seeds are also eaten, taken mainly from the ground (Rotenberry et al. 1999). During the breeding season, Brewer's sparrows apparently take arthropods from sagebrush in proportion to their availability (Stephens 1985, Rotenberry et al. 1999). There is limited information on winter diets; presumably it is primarily composed of seeds (Rotenberry et al. 1999). In the lower Colorado River valley, grass and weed seeds (purslane; *Portulacaceae*), amaranth (*Amaranthaceae*), and goosefoot (*Chenopodiaceae*) made up about 80 percent of their diet (Rosenberg et al. 1991, Rotenberry et al. 1999). Brewer's sparrows drink free water when it is available, yet they are well-adapted to arid environments and appear to adjust readily to water restriction (Rotenberry et al. 1999).

Most detailed information on diet comes from studies of nestling diet. In southeastern Idaho, nestlings were fed butterfly and moth larvae, spiders, true bugs, and leaf hoppers. Brewer's sparrows are significantly less diverse in nestling diet than sage sparrows, with reduced use of flies and grasshoppers (Petersen and Best 1986, Rotenberry et al. 1999). Most of the main food sources for nestlings were shown to be relatively constant from year to year but with annual variations in diet composition likely due to yearly fluctuations in arthropod abundance. There was no seasonal variation in nestling diet or in the size of food items (Rotenberry et al. 1999).

Brewer's sparrows are sensitive to sagebrush control, declining with the loss of shrubs and shifting their diet from insects to seeds in response to the resultant reduction in food availability (Paige and Ritter 1999). No studies have related food resources in fragmented and unfragmented shrubsteppe habitats to differences in Brewer's sparrow productivity.

Breeding biology

The nesting season of the Brewer's sparrow begins with their arrival in spring (from mid-March to early May) and extends to early August, with most nesting activity concentrated between mid-May and late July (Rotenberry et al. 1999). In Colorado, Brewer's sparrows start to arrive in mid-April, with full numbers at the end of the month (Andrews and Righter 1992, Lambeth 1998). Males arrive in breeding areas and begin establishing territories several days before females arrive and pair formation occurs within a few days of the arrival of the females (Best and Petersen 1985, Nordin et al. 1988, Rotenberry et al. 1999). The male becomes less vocal after pairing (Best and Petersen 1985, Rotenberry et al. 1999).

Brewer's sparrows are generally thought to be monogamous, although polygyny has been observed in closely related species (i.e., chipping sparrows [*Spizella passerine*] and field sparrows [*S. pusilla*]). Because males play little role in nest-related activities before the eggs hatch, and because territorial incursions and mate-guarding are common, the potential for extra-pair copulations is high (even though it has not been recorded) (Rotenberry et al. 1999).

Nest site selection begins with pair formation and the female becomes more secretive during the start of the nesting process (Nordin et al. 1988, Rotenberry et al. 1999). Specific nest-site selection behavior has not been described (Rotenberry et al. 1999). Construction of the first nest takes approximately four to five days to complete.

Initiation of egg laying has been observed less than one day after nest completion (Rotenberry et al. 1999). Brewer's sparrows lay one egg per day (typically in the morning), and clutch size is usually three to four eggs, occasionally two and rarely five (Rotenberry et al. 1999). Incubation begins when the last egg is laid and lasts 10 to 12 days. The female incubates; the male frequently remains near the nest, less than 10 m from it, and forages mostly within 50 meters of the nest site.

Hatch dates in Oregon over four years ranged from 30 May to 21 July, the median date was June 27. Both parents brood and feed the nestlings, which typically fledge at six to nine days of age; the majority of young fledge at seven days of age (Rotenberry et al. 1999). The earliest fledge dates in Oregon were 8 June 1979, 16 June 1978, and 18 June 1980, while the latest observed fledging date was 19 July, although other nests likely fledged after 25 July. The chicks are mostly feathered but unable to fly after fledging, and the parents continue to feed them for several days after departure (Rotenberry et al. 1999).

Within the breeding season, Brewer's sparrows will produce replacement clutches when a nest fails, and they frequently double-brood. Renesting begins soon after the loss of the first nest. Second broods are initiated approximately 10 days after the first brood fledges. The proportion of pairs double-brooding and any incidence of triple-brooding have not been reported (Rotenberry et al. 1999).

Demography

Genetic issues

There is no evidence of genetically isolated populations. The extent of dispersal within the breeding range is mostly unknown. Knick and Rotenberry (2002) expect that adult shrubsteppe passerine breeding birds might exhibit strong site tenacity and return after migration to the same breeding territory as the previous year. The return rate of males to the same breeding territory is approximately 25 percent (Rotenberry et al. 1999). In contrast, young birds may seek new areas either following fledging or upon returning from migration (Knick and Rotenberry 2002).

Considering their mostly contiguous distribution, migratory habit, potential for extra-pair copulations, and suspected ability to disperse, Brewer's sparrows may not suffer from genetic issues related to small populations. Brewer's sparrows evolved in, and presumably are adapted to, landscapes dominated by sagebrush that were homogeneous over large spatial scales (Knick and Rotenberry 2002). Consequently, continued fragmentation, isolation of breeding populations, and reduction in numbers may have genetic consequences not yet manifested.

Recruitment, survival, immigration, age at reproduction

Brewer's sparrows breed annually, starting at 1 year of age, and they normally breed each year until death (Rotenberry et al. 1999). The proportion of males that successfully acquire mates varies among years and sites. At one site in Idaho, only 23 percent of the males were successful in a two-year period, while 86 percent were successful during a subsequent five-year period (Petersen and Best 1987, Rotenberry et al. 1999).

The probability of nest success (defined as >1 fledgling produced) varied geographically during a two-year period, ranging from 1 percent in Nevada, 14 percent in Idaho, and 85 percent in Oregon. Nest success also varied temporally, ranging annually in a five-year period from 61 to 100 percent (Rotenberry et al. 1999). Within the same time period, average daily survival rates of nests were 0.81 ± 0.09 SD ($n = 4$) in Nevada and 0.99 ± 0.01 SD ($n = 35$) in Oregon (Rotenberry and Wiens 1989, Rotenberry et al. 1999). Predation of eggs and nestlings was the primary factor affecting nest success, and it was also the primary factor in temporal variation in nest success.

The proportion of total females that rear at least one brood to fledging or independence is estimated to vary annually from 60 to 90 percent in central Oregon. But it may be near zero in areas or years with high nest predation. There is no reported information on lifetime reproductive success (Rotenberry et al. 1999).

Life span is not known, and information on survivorship is not definitive. The proportion of banded males returning to the same breeding site was 25 percent in southeast Idaho and similar in Oregon (Petersen and Best 1987, Rotenberry et al.1999). However, these rates represent a lower limit, as they do not take into account individuals that may be alive and breeding elsewhere (Rotenberry et al.1999).

Lifecycle diagram and model development (prepared with David B. McDonald)

We created a lifecycle graph and constructed a two-stage matrix population model for the Brewer's sparrow. When substantial data are available for a species, demographic modeling can be used to predict population growth rates (λ) under various environmental, demographic, and genetic conditions, providing a measure of the stability (e.g., population viability) of the wildlife population being modeled. However, in cases where data are limited, such as for the Brewer's sparrow, λ cannot and should not be estimated. Yet, modeling exercises (e.g., sensitivity and elasticity analyses) can provide valuable information regarding certain aspects of the population biology of the species of interest. For example, these analyses can improve our understanding of how important specific vital rates are to λ, our ability to identify those vital rates that are the most important for researchers to focus their efforts, and our ability to quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates.

Here, we present a summary of our model results and direct readers to **Appendix A** for the complete methodological considerations and technical analyses. The matrix population analysis was produced with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). Our first exercise was to conduct a sensitivity analysis. Sensitivity is the effect on λ of an absolute change in the vital rates (i.e., survival and fertility). The vital rate to which λ was most sensitive for the Brewer's sparrow was first-year survival. Thus, our major conclusion from the sensitivity analysis is that survival rates, especially first-year survival rates, are most important to population viability. Next, we conducted the elasticity analysis. Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivity analysis. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. The elasticities have the useful property of summing to 1.0. Elasticity analyses for the Brewer's sparrow indicate λ was most elastic to changes in adult survival ($e_{22} = 47.3$ percent ["differential" Variant 1] or 38 percent ["balanced" Variant 2] of total elasticity). Next most elastic were first-year survival and adult reproduction ($e_{21} = e_{12} = 21.5$ percent [Variant 1] or 24.6 percent [Variant 2] of total elasticity), and reproduction by first-year birds was relatively unimportant ($e_{11} = 9.7$ percent [Variant 1] or 19 percent [Variant 2] of total elasticity). The sensitivities and elasticities for the Brewer's sparrow were generally consistent in emphasizing survival transitions. Thus, survival rates, particularly for adults, appear to be the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Finally, we constructed a stochastic model to simulate the effect of environmental variation on λ. The stochastic model produced two major results. First, only high variability on survival rates using the "differential" survival Variant 1 matrix had strong detrimental effects, and second, the magnitude of stochastic fluctuation had a discernible effect on population dynamics. These results indicate that populations of Brewer's sparrow are vulnerable to stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance) when the magnitude of fluctuations is high. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. The Brewer's

sparrow, however, may have little flexibility in reducing variability in first-year survival, which has a relatively high elasticity. Variable early survival is likely to be the rule rather than the exception.

Clearly, improved data on survival rates and age-specific fertilities are needed in order to increase confidence in this demographic analysis. The most important "missing data elements" in the life history of Brewer's sparrow are for survival rates, which emerge as vital rates to which λ is most sensitive as well as most elastic. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations.

Summary of major conclusions from matrix projection model:

- ❖ Survival accounts for 73 percent of the total "possible" sensitivity under the "differential" survival Variant 1 matrix, and 62 percent of the total under the "balanced" survival Variant 2 matrix. Any absolute changes in survival rates will have major impacts on population dynamics.

- ❖ Survival (P_{21} and P_{22}) account for 69 percent ("differential" variant) or 56 percent ("balanced" variant) respectively of the total elasticity. Proportional changes in first-year and especially in "adult" survival will have a major impact on population dynamics.

- ❖ The reproductive value of "adult" females is higher under the "differential" variant (2.8) than under the "balanced" variant (1.6). With the former variant, the higher reproductive value of "adults" makes them possible buffers against the detrimental effects of variable conditions.

- ❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in survival to population dynamics. In comparison to life histories of other vertebrates, the Brewer's sparrow appears slightly less vulnerable to environmental stochasticity (because of the buffering effect of a reservoir of "adult" females and because of the relatively even importance of different vital rates, as assessed by the sensitivities and elasticities).

Ecological influences on survival and reproduction

Weather appears to influence productivity, at least in some populations. Reproductive variables such as clutch size, brood size, and fledgling mass were not sensitive to short-term (i.e., within season) variation in weather experienced at each nest (Rotenberry and Wiens 1991). However, these variables (except fledgling mass) were significantly influenced by large-scale variation in precipitation of the preceding winter (Rotenberry et al. 1999). Increasing precipitation during the preceding winter, which increases ecosystem productivity the following spring, was strongly correlated with increases in clutch size in Oregon. This implies that Brewer's sparrows respond opportunistically by increasing their initial reproductive investment when food is more abundant (Rotenberry and Wiens 1991, Rotenberry et al. 1999). There was significant annual variation in the number of fledglings produced per nest during a five-year study in Oregon (Rotenberry and Wiens 1989). Averages ranged from 1.79 to 3.38 chicks per nest, and the number of fledglings per nest was positively correlated with increasing amounts of precipitation during the preceding winter. Conversely, a six-year study in Idaho found no significant annual variation in the number of fledglings produced per nest (Petersen and Best 1987, Rotenberry et al. 1999).

Nest predation is probably the principal determinant of reproductive success (Rotenberry et al. 1999), and predation rates are apparently affected by fragmentation of sagebrush shrubsteppe habitat. Predation on artificial and natural nests of shrubsteppe birds was higher in fragmented sites than in continuous shrubsteppe sites in eastern Washington, likely due to an increase in corvid populations associated with agricultural and other human-modified habitats. Also, nests might be more difficult to locate in extensive stands of shrubsteppe than in fragmented sites (Vander Haegen et al. 2002).

Spacing, defense and size of area, and population regulation

During breeding the home range and territory are the same. Males are highly territorial during the breeding season and defend their territory for breeding and feeding, although feeding transgressions are more tolerated (Rotenberry et al. 1999). Territory size can vary significantly among sites, between plots within sites, among years, and with plot-year interactions (n

= 3 sites in central Oregon and northern Nevada, 2 plots per site, 2 to 8 years, and 183 territories) (Wiens et al. 1985, Rotenberry et al. 1999). Average breeding territory size ranged from 0.55 to 2.36 hectares (Wiens et al. 1985, Rotenberry et al. 1999), while other reported mean sizes range from 0.10 ha. ± 0.02 SD in central Washington (n = 8; Stephens 1985) to 0.52 ha ± 0.15 SD in southeast Idaho (n = 30; Reynolds 1981, Rotenberry et al. 1999). Territories are most often contiguous with adjacent territories, and they may be tightly packed (Rotenberry et al. 1999). Territory size will contract as densities of breeding birds increase (Wiens et al. 1985). There is no indication that reproductive success is influenced by local density (Rotenberry and Wiens 1989). Likewise, geographic and temporal patterns of variation on population numbers suggest that inter- or intraspecific competition is not important (Rotenberry 1980, Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981a, 1981b).

Dispersal

The extent of initial dispersal of Brewer's sparrows from natal sites is unknown. Of approximately 400 nestlings banded during a seven-year period, none were observed to return to breed near their natal site (Rotenberry et al. 1999). This indicates that either juveniles disperse widely from their natal grounds or suffer high mortality, or both.

Spatial characteristics of populations

BBS data indicate that this species has undergone significant declines throughout the BBS survey area (Rotenberry et al. 1999), including the National Forest System lands in Region 2 (**Table 1**). It is not known whether the populations on the eastern edge of their geographic range, where abundances are lower and they are more patchily distributed, are "sinks", and there may be few, if any, "source" populations (Pulliam 1988). Brewer's sparrows can be thought of as habitat specialists, in that they only occur in sagebrush shrubland habitats, and bird specialists may be poorly equipped to tolerate conditions beyond those experienced in the core of their geographic range (Brown 1995, Pavlacky and Anderson 2001). This may explain the pattern of reduced abundances at the periphery of their range.

Factors limiting population growth

Because Brewer's sparrow populations are affected by events that lie beyond the domain of demographic studies conducted (Knick and Rotenberry 2002), elucidating the processes that regulate population size, causes of population declines, and effects of habitat loss and fragmentation on Brewer's sparrows is problematic. The current hypothesis is that processes operating on the wintering grounds, which are mainly density-independent, regulate population size on the breeding grounds (Rotenberry and Knick 1999, Rotenberry et al. 1999).

Variation in local reproductive success appears to be mainly a function of nest predation, which may have the strongest effect on birth rate (Rotenberry et al. 1999). Levels of nest predation vary significantly both geographically and temporally (Rotenberry et al. 1999). Geographically, in 1976-1977, nest predation ranged from 11 percent of 80 nests in Oregon (Rotenberry and Wiens 1989), 86 percent of seven nests in Idaho (Reynolds 1981), to 100 percent of five nests in Oregon (Rotenberry and Wiens 1989). Temporally, annual nest predation from 1976 to 1980 ranged from 0 to 37 percent in Oregon (Rotenberry and Wiens 1989, Rotenberry et al. 1999). Annual variation in daily nest survival rates for this same time period in Oregon ranged from daily nest survival rates of 0.98 ± 0.01 SD to 1.00 ± 0.01 SD (Rotenberry et al. 1999). The impact of predation outside the breeding season is unknown.

There is some evidence that, at least in part of the Brewer's sparrow's range, nest success is lowered due to increased nest predation by predators associated with agricultural and other human-modified habitats in fragmented landscapes (Vander Haegen et al. 2002). Yet, Knick and Rotenberry (2002) found that individual productivity or probability of predation was not directly related to fragmentation at the level of individual territories. They postulate larger regional patterns of fragmentation may be more important in affecting range-wide dynamics.

Brewer's sparrows are hosts to parasitic brown-headed cowbirds (*Molothrus ater*). Parasitized nests are usually abandoned by the host during incubation; this desertion usually results in the loss of the entire clutch (Rotenberry et al. 1999). Also, because cowbirds usually remove at least one host egg (Rich 1978), the number of host young will be reduced (Rotenberry et al. 1999). The frequency of parasitism varies geographically. In southern Idaho 13 percent (n = 16) of nests were parasitized (Rich 1978); in southeast Washington, 5 percent (n = 281; Vander Haegen and Walker 1999); in central Oregon, 0 percent (n = 110 nests over 5 years; Rotenberry and Wiens 1989); in Nevada, 0 percent (n = 12 nests; Rotenberry and Wiens 1989); and in southeast Alberta, 52 percent (n = 25; Biermann et al. 1987) were parasitized (Rotenberry

et al. 1999). There is no information on the impact of parasitism on host productivity at the population level (Rotenberry et al. 1999).

Other factors may influence productivity. Increasing precipitation during the preceding winter was strongly correlated with increases in Brewer's sparrows' clutch size in Oregon. Reproductive variables such as clutch size, brood size, and fledgling mass were not sensitive to short term (i.e., within-breeding season) variation in weather that each nest experienced (Rotenberry and Wiens 1991, Rotenberry et al. 1999).

Food does not appear to be a limiting factor. Howe et al. (1996) found that reduction of arthropod abundance and biomass did not adversely affect productivity of Brewer's sparrows in Idaho (Rotenberry et al. 1999). In Oregon, the available biomass of arthropods was more than two orders of magnitude greater than required for bioenergetic demands of a community of shrubsteppe birds, including Brewer's sparrows (Rotenberry 1980, Knick and Rotenberry 2002).

Community ecology

Predators and relationship to habitat use

Nest predation is the primary cause of nest failure and is likely to be an important factor in Brewer's sparrow life history traits and habitat use (Rotenberry and Wiens 1989, Rotenberry et al. 1999). Specific differences in Brewer's sparrow habitat use as they relate to the presence/absence and abundance of specific predators have not been reported. Differences in nest predation rates and nest predators in fragmented and continuous habitats have been studied.

One study in eastern Washington (Vander Haegen et al. 2002) examined predation on artificial and actual nests of birds in fragmented and continuous shrubsteppe sites. They found that the predation rate for artificial nests and real nests was greater in fragmented than in continuous shrubsteppe landscapes, a result likely attributable to increased predation by black-billed magpies and common ravens. Small mammals were photographed at nests in both fragmented and continuous landscapes, whereas corvids were photographed depredating nests almost exclusively in fragments. Corvids in shrubsteppe often are associated with agricultural and other human-modified habitats, and Vander Haegen et al. (2002) found a significantly greater abundance of magpies in fragmented landscapes. Ravens were common in both landscapes, and they depredated nests in continuous shrubsteppe. However,

the authors suggest that nests may be more difficult to locate in extensive stands of shrubsteppe than in fragmented sites.

Vander Haegen et al. (2002) did not find an association between patch size and predation rate among their fragment sites. They suggested that predators associated with agricultural lands may move easily through adjacent shrubsteppe (Rotenberry 1998), and the mere presence of agricultural fields or developed lands in the landscape may play a larger part than the size of the fragment in affecting activity of magpies and other generalist predators.

The gopher snake (*Pituophis melanoleucus*) and the Townsend's ground squirrel (*Spermophilus townsendii*) are documented predators of eggs and nestlings. In Oregon, intense, episodic predation of nests was attributed to a marked increase in the density of Townsend's ground squirrels. The irruption of ground squirrels appeared to be triggered by a pattern of drought year followed by two relatively wet years, and nest predation peaked when ground squirrels were most abundant (Rotenberry and Wiens 1989, Rotenberry et al. 1999). Other potential nest predators include loggerhead shrikes (*Lanius ludovicianus*) (Reynolds 1979, Rotenberry et al. 1999), common raven, black-billed magpie, long-tailed weasel (*Mustela frenata*), least chipmunk (*Tamius minimus*), and snakes other than gopher snakes, such as the western rattlesnake (*Crotalus viridis*) (Reynolds 1979, Petersen and Best 1987, Rotenberry and Wiens 1989, Rotenberry et al. 1999). Most of these predators likely prey on adults as well (Rotenberry et al. 1999). In addition, a coachwhip snake (*Masticophis flagellum*) has been reported eating adults (Paine 1968, Rotenberry et al. 1999), and American kestrels (*Falco sparverius*) and prairie falcons (*F. mexicanus*) take adults (Rotenberry et al. 1999).

Competitors

Some information exists that sage sparrows and, perhaps sage thrashers (*Oreoscoptes montanus*), may compete with Brewer's sparrows. Brewer's sparrows are sometimes displaced from a conspicuous song perch by sage sparrows and sage thrashers, both of which are larger and often have overlapping territories with Brewer's sparrows. Either gender of Brewer's sparrow will chase sage sparrows that come within a few meters of the nest site (Rotenberry et al. 1999).

There is no evidence that resources are depressed by densities of other species to the point that it affects

survival or reproduction during the breeding season (Rotenberry 1980, Wiens and Rotenberry 1981a, 1981b, Rotenberry and Wiens 1989, Rotenberry et al. 1999). Nor do geographic and temporal patterns of variation in numbers suggest that interspecific competition is important (Rotenberry 1980, Rotenberry and Wiens 1980b, Wiens and Rotenberry 1981a, 1981b, Rotenberry et al. 1999).

Parasites and disease

Brewer's sparrows are hosts to body parasites including biting lice (Mallophaga), including *Ricinus fringillae* and *R. subdiffusus* (Emerson 1972, Rotenberry et al. 1999). Flesh flies were reported in 4 percent of 69 broods in southeastern Idaho (Petersen et al. 1986), but with no effect on nestling growth or survival. The blowfly (*Protocalliphora braueri*) was reported in 6 percent of 68 broods in central Idaho, with an average of 2.5 larvae per infected nestling (Howe 1991). No fly parasites were observed in 110 broods in central Oregon although they were present in syntopic sage sparrow nests (Rotenberry and Wiens 1989). Likewise, 25 broods in southeastern Alberta had no fly parasites (Biermann et al. 1987, Rotenberry et al. 1999).

Disease in Brewer's sparrows is poorly surveyed (Rotenberry et al. 1999). Of four adults examined, two were infected with the blood protozoan *Haemoproteus* and one with *Haemoproteus* and *Trypanosoma* (Greiner et al. 1975, Rotenberry et al. 1999). Evidence of symbiotic and mutualistic interactions has not been reported.

Envirogram

An envirogram is a tool to depict the proximal and distal causes/components that affect a species' chance to survive and reproduce. Within the envirogram model (**Figure 7**), the environment comprises everything that might influence an animal's chance to survive and reproduce. The envirogram consists of the "centrum" and the "web". Only those things that are the proximate causes of changes in the physiology or behavior of the animal are placed in the "centrum". These are recognized as directly-acting components of the environment. Everything else acts indirectly, through an intermediary or a chain of intermediaries that ultimately influence the activity of one or other of the components in the "centrum". All of these indirectly acting components are placed in the "web" (Andrewartha and Birch 1984).

Within the "centrum", the directly-acting components are classified into four subdivisions according to the animal's response to the component and the consequent reaction of the component to the animal. The four subdivisions are "mates", "resources", "predators", or "malentities". The names "resources" and "mates" refer to well-understood colloquial meanings. "Malentities" differ from "predators" in that they are components that directly affect the animal, causing a decrease in life expectancy or fecundity, but the consequent component activity decreases or does not change. "Predators" also cause a decrease in life expectancy or fecundity in the animal, but, unlike "malentities", the consequent component activity increases. An envirogram depicts the relationships described above. It consists of a dendogram whose branches trace pathways from distal causes in the web to proximate causes in the centrum.

CONSERVATION

Threats

For many decades, range scientists believed that grasslands originally dominated the Intermountain West and that sagebrush invaded because of heavy grazing. As a result, numerous management actions were undertaken to clear sagebrush from areas. More recently it has become evident that sagebrush shrublands, not grasslands, were dominant and widespread, and that the boundaries of sagebrush habitats were generally the same as they are today. Furthermore, it is now recognized that sagebrush habitats provide important habitat to many plant and animal species. In fact, many sagebrush birds, including the Brewer's sparrow, live nowhere else (Paige and Ritter 1999).

Unfortunately, although widespread throughout the west, sagebrush habitats are threatened throughout their range. The synergistic pattern of ground disturbance (due to excessive livestock grazing, failed agriculture, and intentional eradication of sagebrush), fire occurrence, and increased dominance of exotic vegetation, has caused the fragmentation and loss of this habitat to the point that it is one of the most endangered ecosystems in North America (Noss and Peters 1995, Knick and Rotenberry 2002). These changes have potentially compromised the viability of obligate species. Nationally, grassland and shrubland birds show the most consistent population declines over the last 30 years of any group of bird species. Across the U.S. the populations of 63 percent of shrubland and shrub-dependent birds are declining (Paige and Ritter 1999). In the Intermountain West, more than 50 percent of grassland and shrubland bird species show downward population trends (Sauer et al.
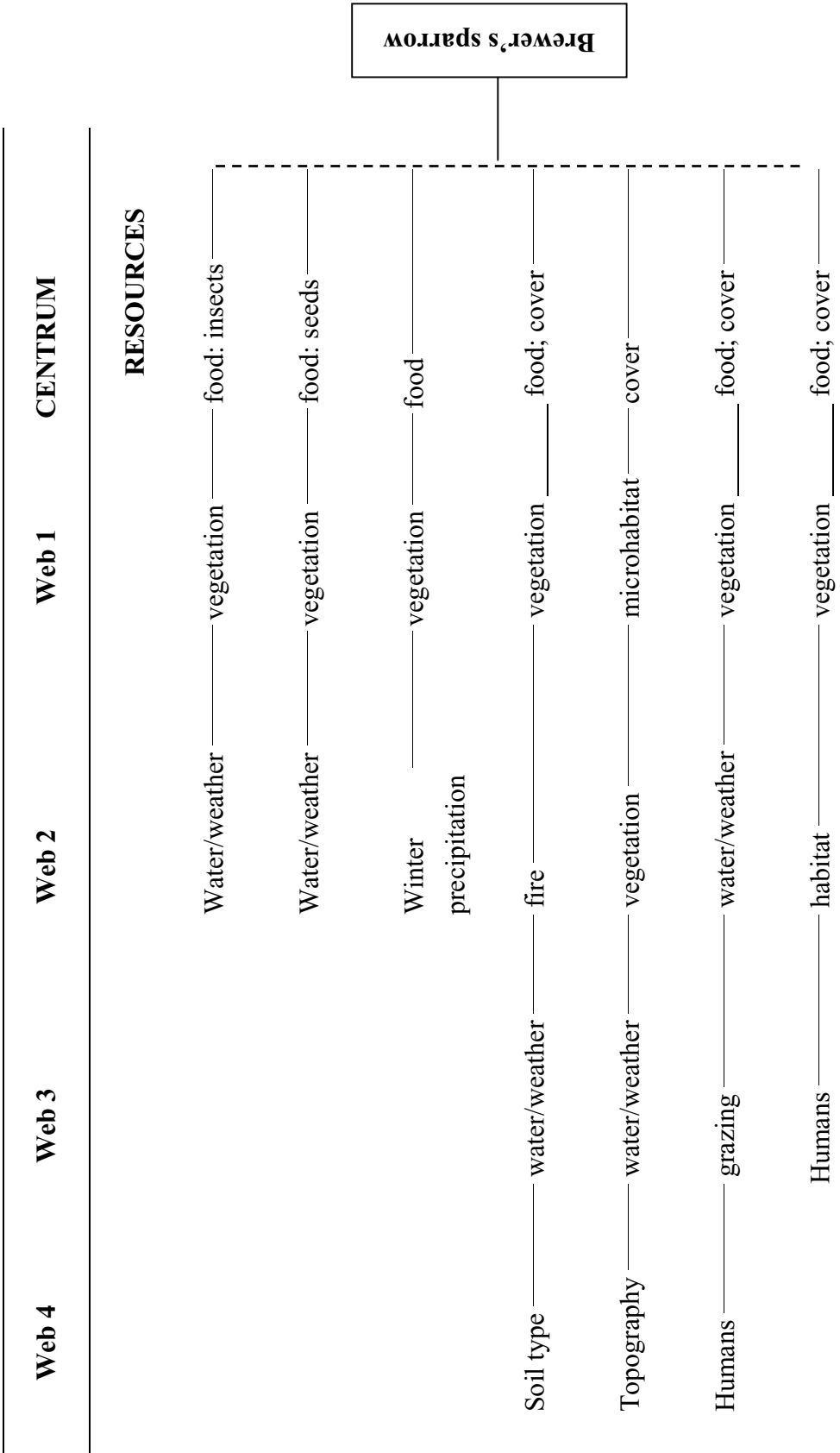
Figure 7a. Resources centrum for the Brewer's sparrow envirogram.

Brewer's sparrow

Web 4	Web 3	Web 2	Web 1	CENTRUM / MALENTITIES
Humans	grazing	water/weather	vegetation	fecundity, densities
Humans	grazing	soil; vegetation	disturbance	fecundity, densities
Humans	sagebrush eradication	fragmentation	vegetation	fecundity, densities
Humans	oil/gas development	fragmentation	disturbance	fecundity, densities
Humans	agriculture	exotic annual grasses	fragmentation/ habitat loss	population decline
Water/ weather	vegetation	food; cover	winter distribution	winter survival
	Water/ weather	vegetation	microclimate	nest phenology
	Water/ weather	vegetation	habitat selection	distribution
	Humans	agriculture	fragmentation/	population decline habitat loss
	Humans	prescribed fire	vegetation	fecundity, densities
		Humans	grazing	nest mortality

Figure 7b. Malentities centrum of the Brewer's sparrow envirogram.

Web 5	Web 4	Web 3	Web 2	Web 1	CENTRUM

PREDATORS/COMPETITORS

Brewer's sparrow

Topography —— water/weather —— vegetation —— microhabitat —— ground squirrel —— predation

Water/weather —— vegetation —— insects/seeds —— ground squirrel —— abundance

Humans —— agriculture —— fragmentation —— corvid abundance

Humans —— grazing —— Brown-headed Cowbird abundance

Figure 7c. Predators/competitors centrum of the Brewer's sparrow envirogram.

1996b). Brewer's sparrows have declined in abundance throughout Region 2.

All of the threats to Brewer's sparrow habitat have complex interactions, making it difficult to separate and prioritize them. We have attempted to order them according to their severity, from the threats that contribute to long-term habitat loss to those that contribute to habitat degradation.

Habitat loss, fragmentation

Large scale reduction and fragmentation of native shrublands have occurred and are occurring and may be responsible for declines in Brewer's sparrows observed on BBS (Rotenberry 1998, Rotenberry et al. 1999). Habitat loss and fragmentation are attributable to a number of activities, including land conversion to tilled agriculture, urban and suburban development, development of road and power-line rights of way, and range improvement programs that remove sagebrush by burning, herbicide application, and mechanical treatment, replacing sagebrush with annual grassland to promote forage for livestock. The pace of the loss and fragmentation has accelerated because of complex interactions among agriculture, livestock grazing, and invasion of exotic plants, especially cheatgrass. Modeling predicts the loss of more than half of the remaining shrublands (Rotenberry 1998, Rotenberry et al. 1999).

The Brewer's sparrow belongs to a group of species that are most typical of undisturbed shrubsteppe. They appear to be especially sensitive to the negative effects of habitat fragmentation (Knick and Rotenberry 1995a, Rotenberry 1998). Among other fragmenting influences, increases in the amount and proximity of agricultural areas in the landscape have been linked with higher rates of nest predation, the primary cause of Brewer's sparrow nest failure. Fragmentation may also reduce sagebrush patch size below a minimum suitable for Brewer's sparrow occupancy.
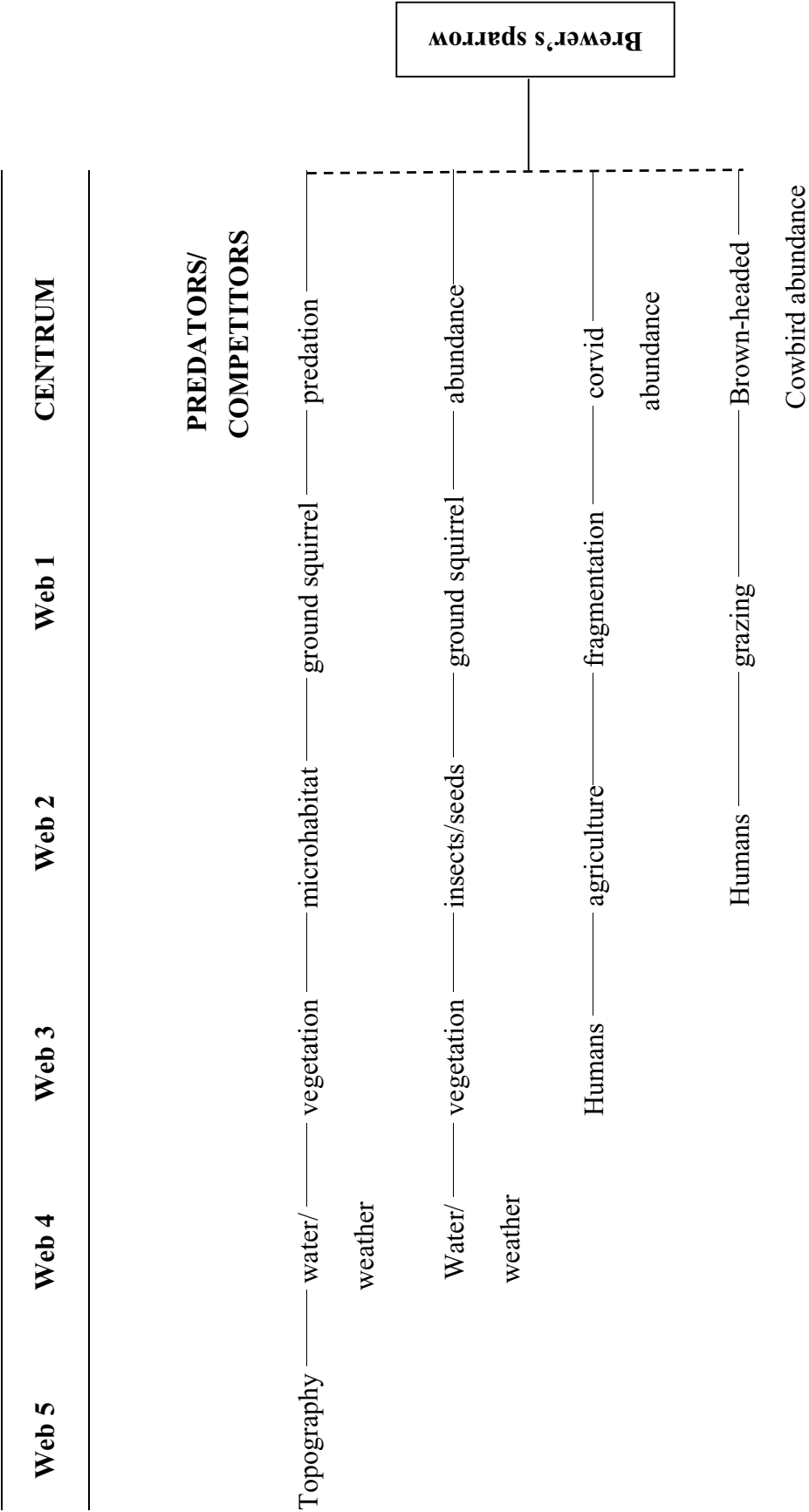
Agriculture

The predominant impact of agricultural development is direct habitat loss due to conversion of shrubland areas to grasslands and croplands, and the subsequent fragmentation of once contiguous shrublands. These losses are long-term in that area, including entire landscapes, that have been converted to agriculture are unlikely to be returned to shrublands in the foreseeable future (Dobler et al. 1996, Vander Haegen et al. 2000, Knick and Rotenberry 2002).

In addition to outright habitat loss, agricultural development has a less obvious but destructive role in the introduction and spread of alien plants into natural habitats; this may now be the most serious threat to these habitats in many areas (Rotenberry 1998). Agricultural areas, and their associated roads, serve as continually renewable sources for immigrant alien species of plants (Janzen 1986, Alberts et al. 1993, Rotenberry 1998). Furthermore, agricultural areas apparently extend the landscape-level distribution of brown-headed cowbirds, which are avian brood parasites, and corvids such as common ravens and American crows, which can be major predators of songbird nests (Marzluff et al. 1994, Robinson et al. 1995, Rotenberry 1998, Vander Haegen et al. 2000).

Invasion of exotic annual grasses and the effects on fire frequency and intensity

Agricultural development, livestock grazing, off-road vehicle use, and road building disturb the soil, which promotes germination of annual plant seeds and, thus, promotes the invasion of exotic annual plants into otherwise undisturbed areas. This process has resulted in perhaps the greatest impact on western shrublands: the establishment of the invasive, exotic cheatgrass. Cheatgrass first appeared in the early to mid-1800s, probably as a contaminant in grain seed (Mack 1981), and it quickly spread among agricultural areas and along roads and railroads. It then spread into otherwise undisturbed shrublands through widespread livestock grazing and the disturbance of the soil surface.

Cheatgrass now occupies millions of hectares of western rangelands, has greatly increased fire frequency, and has substantially, and perhaps permanently, altered postfire successional pathways (Whisenant 1990, Rotenberry et al. 1999). Its principle impact has been to alter the fire ecology of shrubsteppe ecosystems. Cheatgrass provides a continuous surface cover of relatively fine fuel that carries fire into and over much larger areas than likely occurred historically (Whisenant 1990, www.ut.blm.gov/FireRehab). It matures and dries earlier than native bunchgrass, increasing the chance of fire earlier in the season (Knick and Rotenberry 1997). Also, because it does not catch and hold snow like a diverse perennial stand of vegetation, the site becomes drier (desertification; www.ut.blm.gov/FireRehab). In fact, shrublands infested with cheatgrass are 20 times more likely to burn than those without (Stewart and Hull 1949, Whisenant 1990).

With increasing probability of fire, the establishment of cheatgrass reduces the average fire-

return intervals to less than five years, and reduces the chances for sagebrush and native bunchgrasses to regenerate (Whisenant 1990). Post-fire survivorship of cheatgrass is high because it is a winter annual that matures and sets seed by the onset of summer fires, which shatter the seed heads. Conversely, native perennial grasses mature in the summer and have low survivorship after fires. The establishment of cheatgrass in an area makes the area more likely to burn again. Thus, once cheatgrass becomes a part of an ecosystem, it is highly likely to remain a part of it (Rotenberry 1998). Another non-native grass, crested wheatgrass, has also had a role in fundamentally altering the native grass-forb community in many areas of sagebrush shrubsteppe (Whisenant 1990, Rotenberry et al. 1999).

Unlike cheatgrass and other non-native annual grasses, sagebrush after a fire must be re-established by wind-dispersed seeds or by seeds in the soil. A second fire within five to eight years can destroy any viable sagebrush seeds in the seed bank and subsequent recovery of sagebrush can only come from other living sagebrush. Sagebrush seeds disperse about 30 m from a seed source (Meyer 1994, Paige and Ritter 1999). Additionally, sagebrush may take several years to mature before producing seed. Thus, repeated, frequent fires can eliminate sagebrush entirely as cheatgrass becomes established and creates uniform annual grasslands perpetuated by large, frequent fires and void of native plant communities (Whisenant 1990, Paige and Ritter 1999). Restoring native plants is then extremely difficult, if not impossible (West 1996, Paige and Ritter 1999), and the exotic-plant-dominated landscapes that replace native vegetation are uninhabitable for native shrubsteppe-dependent species (Dobkin and Sauder 2004) such as the Brewer's sparrow.

Although cheatgrass and the increased fire frequency associated with its invasion are threats to sagebrush habitats and the species dependent on them, complete fire suppression can also be a threat to healthy sagebrush ecosystems. In some areas, fire suppression and the loss of fine fuels to livestock grazing have resulted in much longer fire-return intervals, and altered the dominant process (i.e., fire) that controlled the shifting temporal and spatial mosaic of grasslands and shrubland characteristic of these landscapes (Dobkin and Sauder 2004).

Within Region 2, sagebrush habitats have not reportedly suffered from altered fire regimes due to invasive annual plants to the degree experienced in the Intermountain West (C. Quimby 2004 personal communication). Still, given that in Colorado the

ecological integrity of sagebrush shrublands has been widely compromised by the invasion of exotic cheatgrass or native pinyon and juniper plant species (Biedleman 2000), the invasion of exotics such as cheatgrass should be considered a threat to Region 2's sagebrush ecosystems.

Prescribed fire

Burning over large areas to eradicate sagebrush is detrimental to Brewer's sparrows because it removes shrub cover, fragments large tracts of sagebrush, and can reduce patch size to levels not used by Brewer's sparrows. It also promotes changes in the vegetative community. Although there is disagreement over the frequency and spatial scale of fires prior to Euro-American settlement, there is uniform agreement that fire frequencies in the Intermountain West have been altered greatly over the last 150 years (Dobkin and Sauder 2004). Altered fire frequencies in combination with the ubiquity of livestock grazing continue to drive the loss of native plant community structure and composition upon which shrubsteppe birds depend.

Mining and oil/gas development

Energy development and natural resource extraction directly alter sagebrush habitats at the site of operation (Braun et al. 2002, Knick et al. 2003). Associated road networks, pipelines, and power transmission corridors fragment habitat and/or create soil conditions facilitating the spread of invasive species (Braun 1998, Gelbard and Belnap 2003, Knick et al. 2003); the cumulative effects of energy development have not been assessed. The density of sagebrush-obligate birds within 100 m of roads constructed for natural gas development was 50 percent lower than at greater distances (Ingelfinger 2001, Knick et al. 2003). Increased numbers of corvids and raptors associated with powerlines also increase the potential impact of predation on sagebrush-breeding birds (Knick et al. 2003). Within Region 2, increasing rates and densities of oil and gas development constitute expanding threats to sagebrush ecosystems. In Wyoming, oil and gas wells have been located primarily in habitats dominated by sagebrush.

Livestock grazing

Livestock grazing has impacted much of the sagebrush habitats across the species' range. The effects of livestock grazing in shrubland habitats are complex, depending on grazing intensity, season, and duration and the extent of alteration to native vegetation.

Livestock grazing impacts sagebrush habitats in several interrelated ways. Its greatest impact is soil disturbance that promotes the germination of annual plant seeds and, thus, promotes the invasion of exotic annual plants into otherwise undisturbed areas. Livestock grazing can lead to other changes in the plant community. Because much of the western shrublands did not evolve under grazing pressure from large ungulates such as bison (*Bison bison*), the impact due to livestock grazing has been detrimental to native vegetation (Mack and Thompson 1982, Rotenberry 1998, Paige and Ritter 1999). As cattle graze sagebrush habitats, they first select grasses and forbs and avoid browsing on sagebrush, which can have a toxic effect on the microorganisms in their rumen (Young 1994). Even light grazing can put pressure on the herbaceous plants favored by livestock (West 1996). Thus, grazing disturbs the soil and results in selective removal of plant biomass, altering competitive relationships among species. This can lead to and increase unpalatable species. Where grazing removes the herbaceous understory altogether, the balance is tipped in favor of unpalatable species, allowing sagebrush to spread and creating dense sagebrush stands with a sparse understory of annuals and unpalatable perennials (Tisdale and Hironaka 1981). While it is not clear that this situation would be detrimental to sage-dependent species, it ultimately discourages livestock use. Throughout the century, this has led to destruction of sagebrush habitats as range managers used fire, herbicides, chaining, and other methods to remove dense sagebrush stands and re-establish grass forage, often reseeding with introduced grass species.

Livestock grazing also destroys the crust that usually forms on the soil and, thus, adversely influences water infiltration, erosion, and nitrogen fixation (Harper and Marble 1988, Rotenberry 1998). This destruction can have long-term effects; recovery from grazing, which includes a well-developed crust community, can take a decade or more, depending on the type of disturbance, the presence of inoculants from nearby crust communities, and the occurrence of invasive weeds (Belnap 1993, St. Clair and Johansen 1993, Kaltenecker 1997, Paige and Ritter 1999). The extent to which soil crusts have been impacted by grazing within Region 2 has not been reported.

In addition to the indirect effects of livestock grazing, it can directly affect Brewer's sparrows during nesting. Livestock trample and disturb nests, resulting in nest failure. Also, the presence of livestock (particularly cattle and horses) can increase the abundance of brown-headed cowbirds, potentially impacting Brewer's sparrow productivity. There is no reported information on cowbird brood parasitism of Brewer's sparrows in Region 2.

Management activities

The influence of management activities and disturbances of Brewer's sparrow habitat have led, in many areas of the West, to large scale conversion of shrublands to grassland habitats dominated by exotic annuals. Much of the sagebrush habitat managed by Region 2 has suffered far less from invasion of exotics and altered fire regimes (C. Quimby 2004 personal communication) than the Intermountain West. Yet, over its geographic range, a large portion of Brewer's sparrow habitat has been negatively impacted. The conversion of landscapes to exotic annual grasslands with high fire frequencies results in changes in the avian composition from communities composed of shrubland obligates (such as the Brewer's sparrow) to those composed of grassland species (such as meadowlarks [*Sturnella* spp.] and horned larks [*Eremophila alpestris*]) (Knick and Rotenberry 1997). Sagebrush habitat has been found to support more species, have a greater bird density and a greater individual density for most species than cheatgrass habitat types (Schuler et al. 1993). This conversion process likely will result in loss of bird species richness and decreased numbers of shrubland-obligate species, including the Brewer's sparrow (Knick and Rotenberry 2002). Correspondingly, the bird species perhaps in the most need of conservation attention are those most typical of undisturbed shrubsteppe including sage grouse (*Centrocercus* spp.), Brewer's sparrow, sage sparrow, black-throated sparrow (*Amphispiza bilineata*), and sage thrasher (*Oreoscoptes montanus*) (Rotenberry 1998, Paige and Ritter 1999).

The threats to Brewer's sparrows and their habitat are widespread across their range, occurring at all spatial scales, from local to landscape to geophysical scales. There are probably other as yet unknown factors contributing to their decline, including factors in wintering areas, and the cumulative effects of habitat disturbance and fragmentation. Many of these threats are interrelated and synergistic and have led to large-scale changes in habitat and have likely contributed to the reported declines of Brewer's sparrows.

Conservation Status of the Species in Region 2

Sufficient evidence exists to suggest that the Brewer's sparrow should be considered a species of high conservation concern in Region 2. Although it has a wide distribution across western North America, in the

Intermountain West more than 50 percent of shrubland and grassland bird species show downward population trends (Sauer et al. 1996a). Brewer's sparrows show declines in abundance throughout Region 2 (Sauer et al. 2003).

Brewer's sparrow life history traits and ecology evolved within a habitat that once experienced little, if any, habitat change within the home range and life span of an individual. They appear to be maladapted for living in a system with rapid, extensive loss and fragmentation due to interrelated and synergistic threats (Knick and Rotenberry 2000, Knick and Rotenberry 2002) and are vulnerable to land use and habitat management practices within the region. There is evidence that fragmentation and changes in habitat patch size affect habitat suitability. Brewer's sparrow numbers are negatively influenced by increasing landscape-level fragmentation of shrublands (Knick and Rotenberry 1995a).

While population declines are fairly well-documented, linkages between habitat variability (due to habitat management) and population viability are poorly understood. How habitat fragmentation influences productivity, density of breeding adults, size of home range, probability of predation or brown-headed cowbird parasitism is not understood (Knick et al. 2003). Our limited understanding of shrubland bird ecology is almost entirely derived from site-specific studies of fine-scale management actions that mostly address short-term effects (e.g., changes in abundance rather than demographic changes) immediately following treatment (Knick et al. 2003). Models developed using site-specific information often do not perform well in regions or times outside of the sampling space (Rotenberry 1986, Knick and Rotenberry 1998, Knick et al. 2003). Additionally, the cumulative effects of habitat variability due to habitat management at different spatial and temporal scales are unknown.

Habitat destruction, degradation, and fragmentation are the chief threats to Brewer's sparrow populations. Agricultural conversion, frequent fire, livestock grazing, and "range improvements" (e.g., shrub removal, exotic grass plantings, etc.) all negatively influence Brewer's sparrow populations. Additionally, these factors frequently promote other impacts, such as exotic species invasion, predation, and nest parasitism (Dobkin and Sauder 2004). The extent to which management activities of the USFS in Region 2 impact Brewer's sparrows versus threats on other areas within the landscape, managed by other entities, is unknown.

Despite the unknowns associated with Brewer's sparrow ecology and its response to threats, it is evident that range-wide, sagebrush habitats on which it depends have been altered by land use, spread of invasive plants, and disrupted disturbance regimes beyond a threshold at which natural recovery of these habitats is likely (Knick et al. 2003). The threats to sagebrush ecosystems are numerous and continue to impact these ecosystems. Some threats (e.g., fragmentation due to road building, recreational use) can be expected to increase in the region. While the likelihood of extirpation of shrubsteppe habitat within Region 2 is low because of its widespread distribution, considering the long-term declines in Region 2 and its specific habitat requirements and ecological characteristics, this species should be a high conservation concern. Action must be taken to increase our knowledge of the conservation status of this species to enable appropriate management action.

Potential Management of the Species in Region 2

Implications and potential conservation elements

In Region 2, long-term declines in Brewer's sparrow populations indicate that existing landscape conditions and management activities are having a negative effect on this species. The overriding essential element for the conservation of the Brewer's sparrow is healthy sagebrush shrubsteppe. Non-native grasses and agricultural and urban conversion now dominate much of western shrublands, making it is especially important to sustain the remaining native sagebrush communities in a healthy state to support native wildlife, including Brewer's sparrow populations (Paige and Ritter 1999, Rotenberry et al. 1999). Conservation of the Brewer's sparrow in Region 2 will require a renewed emphasis on creating the necessary landscape matrix and habitat conditions needed to support this species.

At a regional scale, the maintenance of Brewer's sparrows depends on the existence of extensive tracts of sagebrush shrublands and associated habitat physiognomy, while on a more localized scale, the occurrence and abundance of Brewer's sparrows depend on high sagebrush cover, large patch size, habitat heterogeneity, low disturbance, and little fragmentation. The minimum patch size and degree of patch isolation required for breeding have not been determined. However, Brewer's sparrows do appear to be area-sensitive, and isolated stands of sagebrush

smaller than 2 ha are not likely to be nesting habitat (Knick and Rotenberry 1995a).

Because sagebrush habitats and their dominant disturbance processes vary across Region 2, a simple set of strategic guidelines for Brewer's sparrow management will not work. In general, management of sagebrush landscapes should attempt to mimic the natural disturbance regime (Samson and Knopf 1994). The creation and maintenance of this habitat condition are best accomplished by managing multiple large patches of sagebrush habitat through different or rotating management schemes that ensure the long-term availability of large patches with low disturbance and no fragmentation. Any further conversion of shrublands to agricultural, urban, or suburban development and the resulting fragmentation can be expected to adversely affect Brewer's sparrows. This species will not breed in areas that have been converted to agriculture, and the presence of agricultural and/or housing areas in the landscape can increase nest predation and reduce productivity.

Within sagebrush habitat patches, habitat elements that have been positively correlated with Brewer's sparrow densities (i.e., greater sparrow abundance with increasing amount of the specific element) are the amount of big sagebrush, shrub cover, patches of bare ground, and above-average shrub height. Management activities that reduce shrub cover and fragment shrublands will be detrimental to Brewer's sparrow populations (Wiens 1985, Wiens and Rotenberry 1985, Weins et al. 1986, Dobkin and Sauder 2004).

Conserving native sagebrush habitats will take concerted efforts to prevent the establishment of annual exotic plants in areas that have native understory plants, including the reduction or elimination of the disturbance factors that facilitate the spread of exotic plants (i.e., livestock grazing, road building, and agricultural development). In areas dominated by cheatgrass, efforts will be needed to reduce soil disturbance, reduce fine fuels, determine and re-establish natural fire cycles.

Given the Brewer's sparrow's association with unfragmented sagebrush landscapes and the complexity of disturbance processes, desired conditions may be best managed using a flexible regional scheme that incorporates management approaches based not only on the size and use of the local reserve, but also on the management of nearby reserves and adjacent land use. For example, grazing within the landscape matrix surrounding a reserve that is ungrazed can impact Brewer's sparrows within the reserve by promoting the impact of invasive plants and brown-headed cowbirds. Strategies that encompass public and private lands within the landscape and assess cumulative effects over large spatial and temporal scales will be the most successful in ensuring healthy Brewer's sparrow habitats.

Besides a paradigm shift in habitat management, the successful conservation of the Brewer's sparrow and other sagebrush shrubsteppe birds will require new and innovative strategies that go beyond basic habitat management. Sagebrush habitats on National Forest System lands within Region 2 are relatively healthy and represent an important resource for the conservation of sagebrush-dependent species. However, these lands alone are unlikely to ensure the long-term population viability of this species. There is a significant need to develop partnerships between landowners and state and federal managers that are actively involved in the conservation of sagebrush habitats important to birds. Participation by private landowners may be accomplished through incentive-based programs to conduct agricultural and grazing practices in a manner beneficial to wildlife, but with a reasonable economic cost. Finally, a greater effort is needed to educate the public on the conservation value of healthy, intact sagebrush habitats.

Tools and practices

Inventory and monitoring

Inventory and monitoring populations and habitat. Public lands are managed with an overriding constraint that species, ecosystems, and processes be sustained on the landscape while allowing a variety of other activities to be conducted (Hutto and Young 2002). To ensure that these are being sustained, species population trends must be tracked and the effects of natural and human-caused disturbances must be measured. It is not feasible to monitor every species or every aspect of an ecosystem. However, in some ecosystems monitoring selected birds can be a cost-effective method of assessing ecosystem integrity.

Birds can be good indicators of ecosystem health because they tend to have dynamics that parallel those of the ecosystem; they are sensitive enough to provide an early warning of change and to provide continuous assessment over a wide range of stresses. Birds also have dynamics that can be linked to either natural cycles or anthropogenic stressors. In addition, bird populations are distributed over wide geographical areas and/or are often relatively numerous, so they can be accurately estimated, have costs of measurement that

are not cost prohibitive, have a low impact to measure, and can provide measurable results that are repeatable with different personnel. Because of the relative ease of detection of songbirds such as the Brewer's sparrow, both individual species and communities can be monitored. Thus, birds can serve as informative organisms for measuring natural and anthropogenic changes and for guiding and measuring management and restoration actions (Greenwood et al. 1993, Hutto 1998, Hutto and Young 2002).

Prior to monitoring, an inventory of the biological resource of concern is generally conducted. Bird inventories seek to identify species presence/absence, range, distribution, and relative abundance, and they can provide a baseline for monitoring. Bird monitoring programs are generally developed on this baseline inventory. Commonly, monitoring programs fit into one of two categories: those designed to monitor long-term population trends and those designed to monitor the effects of land management actions. The goals of the monitoring program will affect the methods used. The current Partners in Flight landbird monitoring strategy (Bart and Ralph 2001) recommends integration of long-term monitoring programs and short-term assessments of habitat associations and land-use effects (Hutto and Young 2002).

Species inventory. The initial step in monitoring is conducting an inventory. A species inventory generally consists of conducting systematic surveys to identify the presence and abundance of a species within an area and to document the variables associated with its occurrence, such as habitat type and characteristics. Because information from monitoring can figure so prominently in landbird conservation, it is essential that managers use techniques that can provide "reliable information" (Romesburg 1981). Bird counting techniques that have been used for long-term monitoring can be divided into two groups: (1) methods that use counts or maps of bird detections as an index to relative abundance and (2) detection sampling methods that employ empirical modeling techniques to estimate bird density (Rosenstock et al. 2002). The second group of techniques (i.e., detection sampling) was developed with the recognition that some birds are missed during sampling, making it necessary to incorporate some method of estimating how many birds are missed. These techniques are similar to index counts but have an analytic component that models variation in species' detection to yield direct estimates of density. In practice, the field methods used for detection sampling techniques are basically the same as those used in index counts such as unlimited distance point counts, except that for

each bird heard or seen during the count, the horizontal distance from the observer to the bird is estimated.

There are limitations of detection sampling methods even with the best-trained and most highly skilled observers. In many surveys, for example, the majority of birds are heard but not seen, and the observers estimate the distance to a tree or bush or other object where they think the bird is hiding rather than the actual bird location. Also, distances cannot be estimated accurately in many situations because of habitat complexity, or ventriloqual bird voices, or other reasons. Another drawback to distance sampling is that more than 100 detections are required to develop a good detection function for each species, such that multiple surveys of the same area may be required for all but the most common species in order to get adequate sample sizes (Fancy and Sauer 2000). Thus, detection sampling such as distance sampling is often inappropriate for rare species. However, distance sampling can be easily conducted in appropriate habitats where distances can be reliably measured or estimated, including sagebrush steppe habitats. Density estimates can then be calculated for species detected in sufficient numbers to enable modeling detectabilities.

To conduct robust sampling over the spatial and temporal scales that we view as necessary for adequately monitoring Brewer's sparrows, distance sampling can be used to detect estimates and to describe sources of variation should be used. Recording distance can be facilitated by the use of a laser range finder. These are easy to use in shrubland habitats that have few trees to obscure the view between the observer and the bird. This method would be relatively easy to use for inventorying Brewer's sparrows, and Brewer's sparrows are likely to be detected in sufficient numbers to enable modeling detectabilities and estimating density (Jennifer Holmes, personal observation).

Point count areas for sampling can be established in a variety of ways, depending on the resources available to conduct the inventory. Points can be placed systematically across the landscape or randomly within the landscape. Sampling can also be stratified (e.g., the area is stratified by habitat and random points are selected within each habitat type). In general, there is a trade-off between how many points can be surveyed and how many times each point is surveyed; the greater the number of points, the fewer the number of surveys conducted at each point. There is an advantage to surveying each point more than once in that a greater proportion of the overall breeding season is covered, increasing the probability of sampling during a period

when a particular species' breeding behavior, such as territorial calling and singing, increases their probability of detection.

Population monitoring. Existing programs to monitor distribution and population trends of birds across large areas, such as the BBS (Robbins et al. 1986, Peterjohn and Sauer 1999) and CBC (Root 1988), may not adequately sample many of the species associated with sagebrush ecosystems (Saab and Rich 1997). Even though a high proportion of BBS routes contain sagebrush habitats, the proportional area of sagebrush sampled relative to other habitats along the survey route is far lower. Consequently, BBSs likely capture neither the large-scale habitat features nor the smaller-scale dynamics in the matrix of habitat configurations available to shrubsteppe birds. In addition, surveys based on road networks may limit the researcher's ability to sample population distributions and to estimate abundance over the matrix of available landscapes (Anderson 2001), even though the internal bias due to presence of dirt-tracked or little used roads on bird counts in sagebrush habitats may not be significant (Rotenberry and Knick 1995, Knick et al. 2003). Survey designs need to be based on standard sampling methods for habitats and birds that incorporate local efforts into a broader program in a hierarchical design to address the multi-scale gradients in habitat and bird dynamics (Knick et al. 2003). We suggest using the distance sampling method to monitor long-term population trends in Brewer's sparrows.

These methods fail to provide data on the primary demographic parameters or vital rates (productivity and survivorship) of landbirds. Monitoring the vital rates of Brewer's sparrows, using methods such as constant effort mist-netting or the Breeding Biology Research and Monitoring (BBIRD) protocols (standardized protocols used in a national program for monitoring breeding productivity and habitat conditions for non-game birds; Martin et al. 1997), would make possible the construction of demographic models to assess the viability of populations, aid efforts to identify management actions to reverse population declines, and facilitate evaluating the effectiveness of those remedial management actions. This is because environmental stressors and management actions affect vital rates directly and usually without the buffering or time lags that often occur with population trends. Moreover, habitat- and landscape-specific data on vital rates provide a clear index of habitat and landscape quality and can identify population sources and sinks (Fancy and Sauer 2000).

To assess breeding habitat conditions and nest success, and to estimate densities at small scales, the BBIRD protocol (Martin et al. 1997), which was designed to monitor breeding productivity and habitat conditions for non-game birds using standardized sampling, or modifications of it, are often used. Brewer's sparrows are relatively good subjects for monitoring nest success; several studies (e.g., J.T. Rotenberry, J.A. Wiens, and colleagues in eastern Oregon; L.B. Best, K.L. Petersen, T. Reynolds, and T.D. Rich in southeastern Idaho; W.M. Vander Haegen and colleagues in eastern Washington) were able to acquire relatively large sample sizes of nests within and across sites.

In addition, the technique of constant-effort mist netting and banding (also incorporated in BBIRD protocols) is a tested and proven method for collecting information on vital rates of landbirds. Annual indices of productivity and adult population size can be obtained from analyses of data on the numbers of young and adult birds captured; annual estimates of adult survival rate, adult population size, proportion of residents in the adult population, and recruitment into the adult population can be obtained from modified Cormack-Jolly-Seber analyses of mark-recapture data (Fancy and Sauer 2000).

Inventory and monitoring using focal species. The use of focal species has a number of advantages and disadvantages. The following comments are taken from Chase and Geupel (2003). Advantages of using focal species include the following:

❖ planning and managing for the habitat requirements of every species present in a planning unit is often impractical, if not impossible.

❖ knowledge of the needs of individual species can help direct ecosystem or landscape level planning (Wilcove 1993, Simberloff 1998).

❖ the legal protection assigned to species in the United States (rather than to higher levels of biodiversity, such as habitats, ecosystems, or landscapes) sets up a funding and incentive structure that is species-specific (Noss 1990).

❖ some species are simply much more amenable to monitoring and research than others, a consideration that is crucial given real-life time, logistical, and funding constraints (Chase and Geupel 2003).

There are a number of problems associated with some uses of focal species as well (Landres et al. 1988, Lindenmayer et al. 2002). First, the use of indicator species to assess population trends of other species has been criticized on the grounds that individual species have unique ecological requirements (Taper et al. 1995). Empirical studies have shown that population responses to habitat change often cannot be extrapolated from one species to another, even within the same guild (Landres et al. 1988), or from one population to another of the same species (O'Conner 1992). Second, use of focal species to delineate habitat reserves also may be questionable if focal species do not reliably co-occur with a large proportion of other species in the area of interest (Andelman and Fagan 2000). This assumption is often difficult to test rigorously given our incomplete knowledge of species distributions. For example, Andelman and Fagan (2000) tested the effectiveness of several focal species approaches using species distribution databases from three geographical areas, and they found that most approaches performed poorly. However, these databases contained incidence records only for species with special legal status. The authors were unable to test the effectiveness of schemes that include "non-listed" as well as "listed" focal species and could not evaluate the effect that protecting focal species would have on other "non-listed" species. Third, using species as indicators of habitat quality is only valid if research shows that the density or demographic parameters of focal species are reliably linked to specific habitat, population, or community attributes. Population density alone is known to be an unreliable indicator of habitat quality, even for a single species (Van Horne 1983). Clearly, focal species should be chosen based on explicitly defined criteria, and empirical research and monitoring are needed to validate the assumption that other species are receiving protection as a result of the protection of a focal species (Landres et al. 1988, Noss 1990). As this has become more widely recognized, more empirical tests of focal species approaches have appeared in the literature, with mixed results (e.g., Andelman and Fagan 2000, Chase et al. 2000). A focal species approach should not be the only conservation strategy adopted in a given region, and the effectiveness of all restoration programs should be rigorously tested (Lindenmayer et al. 2002, Chase and Geupel 2003).

Threatened and endangered species are sometimes suggested to be good focal species. These species may be especially sensitive to changes in habitat attributes of concern, but they may not meet the other criteria for effective focal species. For example, the presence of a threatened species, such as the California gnatcatcher

(*Polioptila californica*), often does not indicate the presence of a more diverse or distinctive ecological community (Chase et al. 2000) or the presence of other sensitive taxa (Rubinoff 2001). In some cases, managing for the habitat requirements of an endangered species may not benefit all other species present, and it may even be detrimental to some species or habitats of conservation concern (Launer and Murphy 1994). Also, endangered species that occur at low densities or have regulatory status pose more sampling problems, which may make monitoring less reliable and more expensive (Landres et al. 1988, O'Conner 1992). Even when an endangered species appears to be a good umbrella for co-occurring species, it can be risky to focus conservation emphasis on a single species. If the species can be shown to be more flexible in its breeding requirements than was thought, or if it is found to be genetically indistinguishable from other, less-threatened populations, then the justification for protection of its habitat may be undermined (Chase and Geupel 2003).

Habitat inventory and monitoring. Designing a monitoring program that includes habitat information with sample locations will facilitate the discovery of habitat associations and make a much more effective monitoring program than one based on long-term population trends alone (Hutto and Young 2002). An integrated approach to monitoring both vital rates and population trends of Brewer's sparrows, and relating them to habitat characteristics across the landscape, is critical for understanding causes of population changes and for identifying, as well as testing, management actions and conservation strategies to reverse population declines (Fancy and Sauer 2000). Therefore, habitat inventory and habitat monitoring should be conducted concomitant with a Brewer's sparrow inventory and monitoring program. Vegetation and habitat should be characterized at multiple spatial scales, and measurements of both horizontal and vertical structure should be taken in areas where sparrows are detected and where they are not. Habitat measurements can be coupled with bird inventories to establish species habitat selection within the area of concern. This information can be used as baseline information in subsequent monitoring of long-term avian population trends, and the effects of land use and management actions.

The importance of various vegetation features (breeding habitat attributes) will vary according to species. For Brewer's sparrows, important breeding habitat attributes likely include shrub density for different size classes, percent cover, species composition, measures of patch size, and landscape-level measures such as spatial distribution and distance

between habitat patches, amount of edge, and amount and distribution of agricultural patches.

Monitoring techniques for measuring Brewer's sparrow habitat attributes are not well established. However, identifying habitat relationships for the Brewer's sparrow may better define key habitat attributes (i.e., shrub density) and therefore aid in establishing monitoring methods for this species. The vegetation data collected can document details that are unavailable through remote sensing and may be useful in terms of classifying each point according to elements that are important to Brewer's sparrows, thus explaining any observed changes in Brewer's sparrow density over time (Young and Hutto 2002). Hutto and Young (1999) found that within only a few years, and long before they ever calculated a species population trend, habitat data revealed potential issues of management concern for many species. Even if point-count data suggest that a species is not so specialized, further examination of the habitat relationships can identify critical management issues.

Emphasis should be placed on monitoring variables that are of potential biological importance for Brewer's sparrows (i.e., landscape matrix, patch size, shrub density, prevalence of exotic grasses). The regional extent, distribution, and condition of sagebrush shrublands should be quantified using Geographic Information Systems (GIS) techniques. Specific techniques for measuring within-patch bird habitats should include estimates of structural characteristics of the vegetation at different layers, including horizontal cover (e.g., Daubenmire frames; Daubenmire 1959) and vertical structure. Tree and shrub species composition should also be measured. Within-Patch habitat can be characterized by measuring habitat variables at sampling points within a patch. These habitat measures can be adapted from the field protocols for national or regional programs such as BBIRD (Martin et al. 1997) and the Northern Region Landbird Monitoring Program (NRLMP) of the USFS (Hutto et al. 1998).

Environmental factors (i.e., fire and grazing) that may affect these vegetation characteristics should also be recorded. It is also highly recommended that photo documentation be conducted where point count stations have been established. Photographic documentation could be used to bolster a habitat relationships database for Brewer's sparrows throughout Region 2 (Hutto and Young 1999).

Management approaches

Population or habitat management approaches. The successful management and conservation of Brewer's sparrow populations will depend on the conservation of healthy sagebrush landscapes and the implementation of management actions to restore and conserve degraded areas. In general, management of sagebrush landscapes should attempt to mimic the natural disturbance regime (Samson and Knopf 1994) in order to approximate naturally occurring landscapes. The maintenance of the largest, most continuous stands of sagebrush that exist within Region 2 will benefit Brewer's sparrows, as will small openings (e.g., <1 ha) of short vegetation surrounded by sagebrush (Paige and Ritter 1999).

Too often, historic management of sagebrush habitat has targeted the removal of sagebrush from large areas for reseeding with non-native grasses to increase livestock forage production (Dobkin and Sauder 2004). These practices have been detrimental to Brewer's sparrows and other sage-dependent species. We suggest a suite of approaches to achieve desired conditions for healthy shrubland ecosystems and Brewer's sparrow populations. Some actions taken to protect or restore particular sites will depend on the characteristics of that particular site or landscape. Thus, the following suggestions will need to be adapted to each particular locale, using the expertise of local managers.

There is a need to identify and to protect areas of healthy sagebrush shrubsteppe. Desired environmental conditions include landscapes comprised of all habitats originally, "naturally" occurring (such as a range of seral stages of sagebrush stands, interspersed openings, wet meadows, springs, and healthy riparian habitats) represented across a large area. Practices that permanently convert shrublands to non-native grasslands or agricultural lands should be avoided, as should practices that further fragment areas, such as road building. The cumulative impacts of individual management actions that contribute to fragmentation (e.g., energy development) should be assessed. The creation of edges with converted habitat should be minimized wherever possible. Burning to eradicate sagebrush over large areas (e.g., >20 to 40 ha) should be avoided, and range fires that threaten to eradicate large areas of sagebrush should be suppressed. Providing for "no net loss of sagebrush habitats" (Paige and Ritter 1999) across landscapes will help to achieve the desired

condition of large areas of healthy sagebrush in a landscape that, at least, mimics a natural matrix.

Disturbed sites should be restored or rehabilitated to native plant communities, if possible. Management should move towards the re-establishment of natural disturbance processes and the careful management of practices, such as livestock grazing, which often degrade sagebrush steppe. In some areas, simply protecting areas from degradation may allow for the re-establishment of native plants. In large disturbed areas, however, sagebrush and native perennial grasses may need to be reseeded to shorten the recovery time and to prevent dominance by non-native grasses and forbs. Ecologically appropriate native plant species should be used in all shrubsteppe restoration projects (Knick et al. 2003).

Sources of soil disturbance (e.g., road building, off-road vehicle use, heavy grazing) should be minimized to maintain biological soil crusts, which are sensitive to trampling by humans, vehicles, and livestock (Paige and Ritter 1999). Roads that fragment otherwise continuous sagebrush should be closed or re-routed, if necessary. All vehicles should be kept on established roads and trails or confined within areas established specifically for off-road recreation. These areas should be established so as not to influence sensitive sagebrush habitats and species.

No single grazing strategy is appropriate for all shrubland habitats, and grazing management should be tailored to condition and potential of each grazing unit (Paige and Ritter 1999). Management plans should consider other grazers such as elk and deer, and their influence on the vegetation and stocking levels should enable the stabilization or increase of native perennial groundcover and reduce disturbance to soil crusts. In addition to properly managing stocking levels, grazing seasons and the distribution and types of grazers should be managed to promote native groundcover and to maintain herbaceous cover for nest concealment (Paige and Ritter 1999). For instance, in stands where cheatgrass and native perennial grasses are mixed, grazing during the dormant period may favor perennial species (Vallentine and Stevens 1994, Young 1994, Paige and Ritter 1999). Managing grazing time and intensity can reduce or eliminate trampling of ground nests and nests in low shrubs, such as Brewer's sparrow nests.

Situations that concentrate livestock, such as corrals, feedlots, and watering sites, during the Brewer's sparrow breeding season may increase the impact of brown-headed cowbird brood parasitism on Brewer's sparrow nesting success (Robinson et al. 1995). Rotating livestock use to rest units from cowbird concentrations in alternate years may give local songbird populations breeding opportunities without high parasitism pressure (Paige and Ritter 1999).

Substantial direct and indirect human-induced impacts occur on public lands every year. Although many treatment plans recommend monitoring, the vast majority of these treatments occur without deliberate, well-considered, or funded efforts to examine causal effects on either habitat or associated wildlife (Knick et al. 2003). As management action is undertaken to establish desired environmental conditions of sagebrush shrubsteppe and Brewer's sparrow populations, it is critical to develop and implement pre- and post-treatment designs, including controls, to increase the understanding of the cause-and-effect relationships between land use and changes in habitat and bird communities (Petersen and Best 1999, Anderson et al. 2000, Knick et al. 2003).

Information Needs

A recent review written by experts in the field (Knick et al. 2003) discusses the threats that birds in sagebrush habitats face, synthesizes existing information regarding avifauna of sagebrush habitats, and identifies their management and conservation needs. They conclude that little is understood regarding shrubsteppe bird-habitat dynamics. To manage and conserve birds in sagebrush habitats there is an urgent need for more research into four major topics:

❖ identification of primary land-use practices and their influence on sagebrush habitats and birds

❖ better understanding of bird responses to habitat components and disturbance processes of sagebrush ecosystems

❖ improved hierarchical designs for surveying and monitoring programs

❖ linking bird movements and population changes during migration and wintering periods to dynamics on sagebrush breeding areas.

They found that, in sagebrush ecosystems, we do not understand how habitat fragmentation influences productivity, density of breeding adults, size of home

range, or probability of predation or brown-headed cowbird parasitism.

The general breeding distribution of the Brewer's sparrow is relatively well known. Within its geographic distribution, including within Region 2, distribution patterns, habitat associations, and demographic information within a range of habitat conditions are not well known. Without information on habitat associations, reproductive success, adult and juvenile survivorship, and dispersal patterns, it is impossible to understand and predict the effects of different management options and conservation actions on source-sink dynamics (Knick et al. 2003). The Brewer's sparrow appears to be an area-dependent species, and studies that improve our knowledge of how landscape context influences Brewer's sparrows' sensitivity to habitat fragmentation and nest predation and parasitism rates are also needed. These studies will provide information that can guide conservation planners in determining how large sagebrush conservation areas should be, how they should be spatially arranged, and into what type of landscapes they should be placed (Herkert and Knopf 1998).

In order to study the effects of management approaches, such as grazing, experiments having strong statistical designs that include treatments and controls at spatial and temporal scales relevant to the impacts to vegetation and soils and the dynamics of recovery are needed (Knick et al. 2003). Long-term studies incorporating a widespread system of exclosures and the ability to control treatment levels are necessary to measure the effects of land use on habitats and birds. Knick et al. (2003) suggest that treatment projects planned by management agencies, and the large number of areas to be treated, represent a tremendous opportunity to design a sound experimental approach. Establishing such studies and combining them with monitoring at appropriate scales would provide the feedback to evaluate treatment effects and provide the basis for adaptive management strategies (Walters 1986, Morrison 2002, Knick et al. 2003). Such information is critical for identifying causes of population changes and for testing management actions and conservation strategies to reverse population declines.

DEFINITIONS

Bird Conservation Region — ecologically distinct regions in North America with similar bird communities, habitats, and resource management issues within which bird conservation efforts are planned and evaluated, as endorsed by the North American Bird Conservation Initiative (2000).

Physiographic Area — Partners in Flight planning units defined on the basis of biotic communities and bird distribution; used in bird conservation planning.

Physiographic Stratum — Breeding Bird Survey regional areas defined on the basis of similar vegetation, soil, and physiographic features and used in analysis of bird species' population trends and relative abundance.

USDA Forest Service Region 2 (Rocky Mountain Region) — Wyoming, Colorado, South Dakota, Nebraska, and Kansas (**Figure 1**).

U.S. Fish and Wildlife Service Region 6 (Mountain-Prairie Region) — Wyoming, Colorado, South Dakota, Nebraska, Kansas, Montana, Idaho, and Utah.

U.S. Fish and Wildlife Service Region 2 (Southwest Region) — Arizona, Oklahoma, New Mexico, and Texas.

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APPENDIX A

Matrix model development for the Brewer's Sparrow

Lifecycle diagram and model development (prepared with David B. McDonald)

The studies of Petersen and Best (1987), Rotenberry and Wiens (1989), Rotenberry and Wiens (1991), Rotenberry et al. (1999), and Knick and Rotenberry (2002) provided the basis for formulating a lifecycle graph for Brewer's sparrow that comprised two stages (censused at the fledgling stage and "adults"). We used the mean fledging rate of 1.25 female fledglings per female of Rotenberry et al. (1999) as the basis for calculating fertilities. Because of a lack of data, we did not assume a change in fertility with age, an assumption that is often justified in avian demography (Ricklefs 1973, McDonald and Caswell 1993). The only estimates of survival for this species were the minimum rate of 0.25 for males noted by Rotenberry et al. (1999), so we used a bracketed system of large and small difference between first-year and "adult" survival as the basis for estimated survival rates. Our initial variant (Variant 1 – which we will refer to as the "differential survival" variant) assumed that first-year and "adult" survival were quite different ($P_{21} = 0.25$, $P_a = 0.69$), with the values adjusted until population growth rate (λ) = 1.003. This "missing element" method (McDonald and Caswell 1993) is justified by the fact that, over the long term, λ must be near 1.0 or the species will go extinct or grow unreasonably large. The alternative model (Variant 2 – "balanced survival") assumed that first-year survival ($P_{21} = 0.35$) was more similar to "adult" survival ($P_a = 0.565$). From the resulting lifecycle graphs (**Figure A1**, **Figure A2a**, and **Figure A2b**), we produced a matrix population analysis with a post-breeding census for a birth-pulse population with a one-year census interval (McDonald and Caswell 1993, Caswell 2001). The models had two kinds of input terms: P_i describing survival rates, and m_i describing number of female fledglings per female (**Table A1**). **Figure A2a** shows the symbolic terms in the projection matrices corresponding to the life cycle graphs for both variants. **Figure A2b** and **Figure A2c** give the corresponding numeric values for the two variants. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female; thus, the fledgling number used was half the total annual production of fledglings, assuming a 1:1 sex ratio. Note also that the fertility terms (F_i) in the top row of the matrix include both a term for fledgling production (m_i) and a term for the survival of the mother (P_i) from the census (just **after** the breeding season) to the next birth pulse almost a year later. λ was 1.003 for both variants, based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value was used as an assumption for deriving a vital rate, and should not be interpreted as an indication of the general well-being of the population. Other parts of the analysis provide a better guide for assessment.
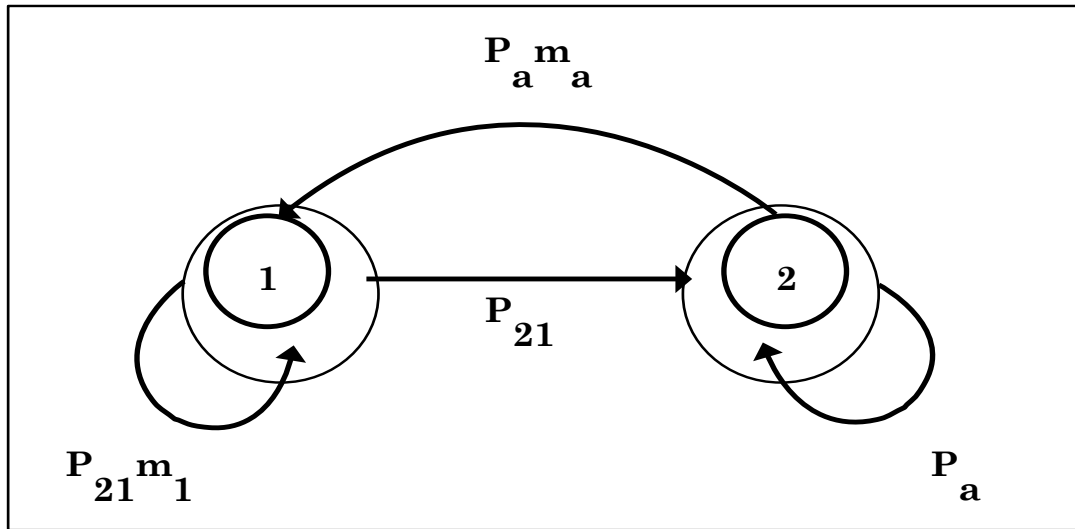

Figure A1. Lifecycle diagram for the Brewer's sparrow. The numbered circles ("nodes") represent the two stages (first-year birds and "adults"). The arrows ("arcs") connecting the nodes represent the vital rates — transitions between age-classes such as survival (P_{ji}) or fertility (the arcs pointing back toward the first node).

	1	2
1	$P_{21}m$	$P_a m$
2	P_{21}	P_a

Figure A2a. Symbolic values for the projection matrix of vital rates, **A** (with cells a_{ij}) corresponding to the Brewer's sparrow life cycle graph of **Figure A1**. Meanings of the component terms and their numeric values are given in **Table A1**.

	1	2
1	0.313	0.863
2	0.25	0.69

Figure A2b. Numeric values for matrix Variant 1, assuming a high "differential" between first-year and "adult" survival rates.

	1	2
1	0.437	0.706
2	0.35	0.565

Figure A2c. Numeric values for matrix Variant 2, assuming more "balanced" first-year and "adult" survival rates.

Table A1. Parameter values for the component terms (Pi and mi) that make up the vital rates in the projection matrix for Brewer's sparrow.

Parameter	Numeric value	Interpretation
M	1.25	Number of female fledglings produced by a female
P_{21}	0.25 or 0.35	First-year survival under the "differential" and "balanced" variants
P_a	0.69 or 0.57	Survival rate of "adults" under the "differential" and "balanced" variants

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on λ of an **absolute** change in the vital rates (a_{ij}, the arcs in the lifecycle graph [**Figure A1**] and the cells in the matrix, **A** [**Figure A2a**]). Sensitivity analysis provides several kinds of useful information (see Caswell 2001, pp. 206-225). First, sensitivities show how important a given a vital rate is to λ, which Caswell (2001, pp. 280-298) has shown to be a useful integrative measure of overall fitness. One can use sensitivities to assess the relative importance of survival (P_i) and fertility (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large

sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest. **Figure A3a** shows the "possible sensitivities only" matrices for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible — for example, the biologically impossible sensitivity of λ to the transition from Stage 2 "adult" back to being a Stage 1 first-year bird).

The summed sensitivity of λ to changes in survival is lower under the balanced survival Variant 2 model (61.8 percent of total sensitivity accounted for by survival transitions) than in the differential survival Variant 1 model (73.4 percent of total). Under either variant, first-year survival is more important than is

	1	2
1	0.312	0.249
2	0.86	0.688

Figure A3a. Possible sensitivities only matrix, $\mathbf{S}_p$ for the "differential" survival Variant 1 matrix (blank cells correspond to zeros in the original matrix, **A**). The λ of Brewer's sparrow is most sensitive to changes in first-year survival and fertility (Cell $s_{12} = 0.86$).

	1	2
1	0.436	0.349
2	0.704	0.564

Figure A3b. Possible sensitivities only matrix, $\mathbf{S}_p$ for the "balanced" survival Variant 2 matrix (blank cells correspond to zeros in the original matrix, **A**). Under this variant, the λ of Brewer's sparrow is most sensitive to changes in first-year survival (Cell $s_{21} = 0.704$) followed by changes in "adult" survival (Cell $s_{22} = 0.564$).

"adult" survival (**Figure A3a** and **Figure A3b**). The major conclusion from the sensitivity analysis is that survival rates, especially first-year survival rates, are most important to population viability when changes in the vital rates are absolute (as opposed to proportional, as discussed below in the section on elasticity analysis).

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, an absolute change of 0.5 in survival may be a large alteration (e.g., a change from a survival rate of 90 percent to 40 percent). On the other hand, an absolute change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to **proportional** changes in the vital rates (a_{ij}) and thus partly avoid the problem of differences in units of measurement (for example, we might reasonably equate changes in survival rates or fertilities of 1 percent). The elasticities have the useful property of summing

to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species. It is important to note that elasticity as well as sensitivity analysis assumes that the magnitude of changes (perturbations) to the vital rates is small. Large changes require a reformulated matrix and reanalysis.

Elasticities for Brewer's sparrow are shown in **Figure A4a**. λ was most elastic to changes in "adult" survival for both variants ($e_{22} = 47.3$ percent ["differential" Variant 1] or 31.8 percent ["balanced" Variant 2], where the e_{22} is the percentage of total elasticity on arc P_{22}, the self-loop from the second node back to the second node in **Figure A4b**). Next most elastic were first-year survival and "adult" reproduction ($e_{12} = e_{21} = 21.5$ percent [Variant 1] or 24.6 percent [Variant 2] of total elasticity).

	1	2
1	0.097	0.215
2	0.215	0.474

Figure A4a. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the "differential" survival Variant 1 matrix. The λ of the Brewer's sparrow is most elastic to changes in "adult" survival ($e_{22} = 0.474$), followed by "adult" fertility and first-year survival ($e_{12} = e_{21} = 0.215$).

	1	2
1	0.191	0.246
2	0.246	0.318

Figure A4b. Elasticity matrix, **E** (remainder of matrix consists of zeros) for the "balanced" survival Variant 2 matrix. The λ of the Brewer's sparrow is most elastic to changes in "adult" survival ($e_{22} = 0.318$), followed by second-year fertility and first-year survival ($e_{12} = e_{21} = 0.246$). Under this variant, the relative importance of each of the four kinds of transitions (vital rates) is more even than under the "differential" model (e.g., "adult" survival is only 1.7 times as great compared to a 4.9 fold difference under the "differential" variant).

Least important was reproduction by first-year birds (9.7 or 19 percent respectively of total elasticity). The sensitivities and elasticities for Brewer's sparrow were generally consistent in emphasizing survival transitions with the elasticities strongly emphasizing adult survival, whereas the sensitivity analysis gave a slight edge to first-year survival. Thus, survival rates, particularly "adult" survival rates, are the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Other demographic parameters

The **stable stage distribution** (SSD, **Table A2**) describes the proportion of each age-class or stage in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable stage distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals.

For Brewer's sparrow at the time of the post-breeding annual census (just after the end of the breeding season), fledglings represent 55.6 percent of the population (regardless of model variant used). **Reproductive values** (**Table A3**) can be thought of as describing the value of a stage as a seed for population growth relative to that of the first (newborn or, in this case, fledgling) stage (Caswell 2001). The reproductive value of the first stage is always 1.0. An "adult" female individual in Stage 2 is "worth" 2.8 fledglings under the "differential" survival model of Variant 1, but worth only 1.6 fledglings under the "balanced" survival Variant 2. The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The "adult" females are therefore important stages in the life cycle, particularly if the "differential" Variant 1 more closely depicts the actual demographic condition of Brewer's sparrows. The cohort generation time for this species was 3.2 years (SD = 2.7 years) under the "differential survival" Variant 1 and 2.3 years (SD = 1.7 years) under the "balanced survival" Variant 2.

Table A2. Stable age distribution (right eigenvector). At the census, 57 percent of the individuals in the population should be fledglings. The rest will be older "adult" females (yearlings or older).

Stage	Description	Proportion	Mean age (± SD) Variant 1	Mean age (± SD) Variant 2
1	Fledglings (to yearling)	0.566	0 ± 0	0 ± 0
2	"Adult" females	0.444	3.2 ± 2.7	2.3 ± 1.7

Table A3. Reproductive values (left eigenvector). Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value (second-year females) is highlighted.

Stage	Description	Variant 1 ("differential")	Variant 2 ("balanced")
1	Fledglings/first-year females	1.0	1.0
2	"Adult" females	2.8	1.6

Stochastic model

We conducted a stochastic matrix analysis for Brewer's sparrow. We incorporated stochasticity in several ways (**Table A4**), by varying different combinations of vital rates, by varying the amount of stochastic fluctuation and by varying the "base matrix" (the "differential" or "balanced" survival variants of **Figure A2a** and **Figure A2b**). We varied the amount of fluctuation by changing the standard deviation of the truncated random normal distribution from which the stochastic vital rates were selected. To model high levels of stochastic fluctuation we used a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Under Case 1 we subjected both fertility arcs (F_{11} and F_{12}) to high levels of stochastic fluctuations (SD one quarter of mean) using the "differential" survival Variant 1 matrix. Under Case 2 we varied both survival arcs (P_{21} and P_{22}) with high levels of stochasticity (SD one quarter of mean), again with the "differential" Variant 1 matrix. Under Case 3 we again varied survival with high levels of stochastic fluctuation, but using the "balanced" survival Variant 2 matrix. Case 4 varied survival with "differential" survival Variant 2 matrix, but with only half the stochastic fluctuations (SD one eighth of mean). Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Stage Distribution (SSD) under the deterministic model. Beginning at the SSD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell (2001), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (**Table A4**) produced two major results. First, only high variability on survival rates using the "differential" survival Variant 1 matrix had strong detrimental effects. For example, 87 of 100 runs led to extinctions with stochasticity affecting both survival rates and acting on the low first-year survival matrix (Case 2). The next greatest effect came from stochastic survival for the "balanced" survival Variant 2 matrix (Case 3), which had 32 extinctions. The difference in the effects of which arc was most important is predictable largely from the elasticities. λ was most elastic to changes in survival, especially under the "differential" survival variant. This detrimental effect of stochasticity occurs despite the fact that the average vital rates remain the same as under the deterministic model — the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2001). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. Second, the magnitude of stochastic fluctuation has a discernible effect on population dynamics (compare Variants 2 and 4 in **Table A4**).

Table A4. Results of four cases of different stochastic projections for Brewer's sparrow. Stochastic fluctuations have the greatest effect when acting on survival rates for the "differential survival" variant (Case 2).

	Case 1 (Variant 1)	Case 2 (Variant 1)	Case 3 (Variant 2)	Case 4 (Variant 1)
Input factors:				
Affected cells	F_{11} and F_{12}	P_{21} and P_a	P_{21} and P_a	P_{21} and P_a
S.D. of random normal distribution	1/4	1/4	1/4	1/8
Output values:				
Deterministic λ	1.003	1.003	1.003	1.003
# Extinctions/100 trials	0	87	32	0
Mean extinction time	N.a.	1,185	1,514	N.a.
# Declines/# surviving populations	34/100	13/13	56/68	38/100
Mean ending population size	1.3×10^6	635	73,064	4.6×10^6
S.D.	5.6×10^6	1,313	467,808	2.6×10^7
Median ending size	28,822	75	367	27,825
Log λ_s	0.0008	-0.0082	-0.0036	0.0005
λ_s	1.0008	0.9918	0.9964	1.0005
Percent reduction in λ	0.17	1.06	0.6	0.2

With low level of stochastic variation directed at the "differential" survival variant, no populations went extinct, although 38 of 100 underwent declines (vs. 87 extinctions and all 13 surviving populations declining under the high stochasticity case). These results indicate that populations of Brewer's sparrow are somewhat vulnerable to high levels of stochastic fluctuations in survival (due, for example, to annual climatic change or to human disturbance). This effect will be especially pronounced if the difference between first-year and "adult" survival is fairly large, as in our "differential" variant. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. Brewer's sparrow, however, may have little flexibility in reducing variability in first-year survival. Variable early survival is likely to be the rule rather than the exception.

Potential refinements of the models

Clearly, data on survival rates are needed in order to increase confidence in any demographic analysis. The most important "missing data elements" in the life history for Brewer's sparrow are for survival rates, which emerge as vital rates to which λ is sensitive as well as most elastic. For example, do survival rates vary with rainfall, as fledging success seems to do? Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of "stochastic" matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variations in vital rates. Using observed correlations would improve on our "uncorrelated" assumption, by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history

traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.

Summary of major conclusions from matrix projection models

❖ Survival accounts for 73 percent of the total "possible" sensitivity under the "differential" survival Variant 1 matrix, and 62 percent of the total under the "balanced" survival Variant 2 matrix. Any absolute changes in survival rates will have major impacts on population dynamics.

❖ Survival (P_{21} and P_{22}) account for 69 percent ("differential" variant) or 56 percent ("balanced" variant) respectively of the total elasticity. Proportional changes in first-year and especially in "adult" survival will have a major impact on population dynamics.

❖ The reproductive value of "adult" females is higher under the "differential" variant (2.8) than under the "balanced" variant (1.6). With the former variant, the higher reproductive value of "adults" makes them possible buffers against the detrimental effects of variable conditions.

❖ Stochastic simulations echoed the elasticity analyses in emphasizing the importance of variation in survival to population dynamics. In comparison to life histories of other vertebrates, Brewer's sparrow appears slightly less vulnerable to environmental stochasticity (because of the buffering effect of a reservoir of "adult" females and because of the relatively even importance of different vital rates, as assessed by the sensitivities and elasticities).